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Feeding and Foraging Behaviors of Subterranean Termites (Isoptera:Rhinotermitidae).

Keith Scott Delaplane
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Feeding and foraging behaviors of subterranean termites (Isoptera:Rhinotermitidae)

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FEEDING AND FORAGING BEHAVIORS OF SUBTERRANEAN TERMITES (ISOPTERA: RHINOTERMITIDAE)

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

The Department of Entomology

by
Keith Scott Delaplane
BS, Purdue University, 1983
MS, Louisiana State University, 1986
December, 1989

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After five years and two degree programs at Louisiana State University, I have many fond memories of loved ones, friends, and teachers who enabled it all. Being prone to morbid pessimism, I was refreshed frequently by the words of my wife, Mary, who reminded me how good I really had it. My all-too-distant parents on the farm in Indiana learned the jargon of graduate school and followed my progress enthusiastically. Our dear friends at Southside Baptist Church became surrogate family and spiritual teachers. My bagpipe teacher, Martin Schreiber, in response to my second thoughts about entomology, said, "Don't quit; we *need* bug experts in Louisiana."

Jimmy Carroll was my most faithful student worker, and his labors are represented throughout this dissertation. The Louisiana Pest Control Association funded all my research.

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interjected enough direction to give it focus. Dr. La Fage was a comprehensive repository of scientific and applied information. Paraphrasing the words of Bob Danka, he could "discourse on apterygote tentoria then consult a pest control operator about a problem account." He would have savored my completion of this degree, since I am his first graduating PhD student. He will be remembered by many and very much so by me.

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ABSTRACT

Six studies were done on feeding and foraging behaviors of three species of subterranean termites, *Coptotermes formosanus* Shiraki, *Reticulitermes flavipes* (Kollar), and *R. virginicus* (Banks) (Isoptera: Rhinotermitidae).

When presented with four equal wood blocks, *C. formosanus* did not forage randomly but concentrated on a few preferred blocks. When *R. flavipes* and *C. formosanus* were each placed in foraging arenas with linear, successive wood blocks, *C. formosanus* consumed a greater percentage dry mass of a wood block before moving to the next block (10.3%) than did *R. flavipes* (4.2%).

Groups of *C. formosanus* were offered wood blocks that differed in initial moisture content. Wood feeding rate, number of workers, and number of soldiers were highest in the high moisture treatment. Large changes in wood moisture occurred and were affected by the presence of termites. Groups of termites from five colonies of *C. formosanus* were presented with wood blocks that had been previously damaged: 1) by nestmates, 2) by conspecifics from another colony, 3) by *R. virginicus*, and 4) no damage. *Coptotermes formosanus* preferred wood previously damaged by conspecifics, regardless of colony origin, over wood damaged by *R. virginicus* or undamaged wood. Additionally, they preferred wood damaged by *R. virginicus* over undamaged wood.

Wood surface area (mm^2) exposed per unit feeding was

higher for *C. formosanus* and *R. flavipes* than for *R. virginicus*. Wood surface area was sometimes reduced, rather than increased, as a result of feeding by *R. virginicus*.

Groups of *C. formosanus* were dyed with 0%, 0.5% or 1% concentrations of the dye, Sudan Red 7B. Dyed termites had lower numbers of symbiotic protozoans, lower feeding rates, and lower survivorship than did non-dyed termites.

These studies suggest that toxic baits for remedial control of termites should be placed at areas of strong foraging since termites are predisposed to stay at rewarding sites. Baits should be highly moist. Areas of structures with previous termite damage should be carefully monitored for reinfestation.

These species may differ in their roles as wood decomposers. The popular termite marker, Sudan Red 7B, is not totally innocuous to *C. formosanus*.

INTRODUCTION

Termites belong to the insect order Isoptera. All termites are eusocial, demonstrating cooperative brood care, reproductive division of labor, and overlap of generations (Wilson, 1971). Most termites eat some form of cellulose, a carbohydrate that is nutritionally unavailable to most other animals. This specialized trophic niche and a cryptic colonial life history that buffers reproductives from stress are important reasons for the long and successful history of these insects; termites may have arisen as early as the Permian period (Wilson, 1971). A dietary specialization with cellulose has costs. Wood is a poor source of nitrogen (Swift & Boddy, 1984), and this deficiency may explain the slow growth rates of incipient colonies (Brian, 1965).

As wood-feeders, termites are valuable detritiphores. The channelizing activities of termites and other wood-boring insects in dead wood essentially regulate later decay processes (Ausmus, 1977). Termites may consume up to 28% of the world's annual net primary productivity (Zimmerman *et al.*, 1982).

The Isoptera are mostly tropical insects. Of the four termite families in North America, the Rhinotermitidae are the most widely dispersed. This family originated in the Oriental zoogeographic region, perhaps from an extinct hodotermitid ancestor. Coptotermitinae, with one genus *Coptotermes*, is the most primitive subfamily and probably was ancestral to the

Heterotermitinae which include the temperate genus *Reticulitermes* (Krishna, 1970). Three rhinotermitids, *Coptotermes formosanus* Shiraki, *Reticulitermes flavipes* (Kollar), and *R. virginicus* (Banks), are addressed in this dissertation.

According to Abe (1937), the Formosan subterranean termite, *Coptotermes formosanus* Shiraki, was first described in 1909 from Formosa (Taiwan). Its alates are yellowish colored night-flyers and have many setae on the wings. With 48 species (Roonwal, 1970), *Coptotermes* is a large genus by termitological standards, and some believe its taxonomy is in poor condition. Watson *et al.* (1984) suggested that *C. formosanus* is a complex of species, noting the uncertain relationship between it and *C. vastator* Light from the Philippines. However, in North America *C. formosanus* has shown high homogeneity of allozyme (A. K. Korman, pers. comm.) and DNA (J. Spatafora, pers. comm.) characters, strongly suggesting the singularity of this species in the United States. *Coptotermes* spp. are easily spread by man's commerce, and now they are virtually cosmotropical (Chhotani, 1985). Although *C. formosanus* was originally described from Taiwan, it was probably introduced there from mainland China. Recently, a staphylinid inquiline was described from nests of *C. formosanus* near Shanghai and Guangzhou (Kistner, 1985). Kistner argues that such termitophiles are rarely exported with termites because this requires that the entire nest be

moved. Consequently, the discovery of such an inquiline is strong evidence for the endemic placement of *C. formosanus* in mainland China.

The recognized initial introduction of *C. formosanus* in the United States occurred in Houston, TX in 1965 (Spink, 1967). However, Chambers (1988) reported a rediscovered sample of *C. formosanus* from Charleston, SC, dated 26 March 1957, that was originally mis-identified by T. E. Snyder as *Incisitermes schwarzi* Banks. This new information changes the historical interpretation of the spread of this termite in the United States. In Louisiana, heavy infestations of *C. formosanus* were first discovered in New Orleans and Lake Charles in 1966 (Spink, 1967). Judging from the maturity of the colonies and their proximity to military bases, termite specialists generally agree that this termite was introduced to the United States by naval traffic following World War II and "incubated" for about 12 years before being noticed.

Coptotermes formosanus, like all termites, are weak flyers, and their swarming reproductives travel only a few meters from the parent nest. However, because of the ability of this termite to spread in transported wood or soil, isolated infestations have occurred in Memphis, TN (Robinson, cited in Chambers, 1988), Ocean Springs and Meridian, MS (Jones, cited in Chambers, 1988), Hallandale, FL (Thompson, 1985), Lafayette, LA (La Fage, 1987), and Auburn, AL (Sponsler *et al.*, 1988). Where this species occurs it is usually the

most serious urban pest, owing to its large colony size, voracious appetite for wood, and tendency to locate colonies in inaccessible wall voids.

Reticulitermes flavipes (Kollar) was described as *Termes flavipes* in 1837 "from the Imperial Hothouses at Schönbrunn near Vienna, Austria" (Snyder, 1926). This population was doubtless an accidental introduction from North America where *R. flavipes* is common; in Europe today, this species persists in only a few locations near Salzburg (Harris, 1970). Its alates are dark colored day-flyers, and their ocelli are located more than one ocellus diameter from the compound eye.

R. flavipes is the most economically important termite in the United States. Essentially southeastern in foci, it ranges westward to eastern Kansas and north to Toronto (Weesner, 1970). Its northward spread seems to be encouraged by the increased use of central heating in structures, but there is evidence that it also spreads through contaminated wood and soil (Grace, 1987) as does *C. formosanus*. Losses from control and structural repair due to *R. flavipes* were $435.3 million in the southeastern states in 1983 (Hamer, 1985). Throughout its range, *R. flavipes* is the most serious termite pest except for areas where its range overlaps that of *C. formosanus*. In New Orleans, LA and Broward County, FL, *C. formosanus* displaces *R. flavipes* as the primary termite pest (Su & Scheffrahn, 1988).

Reticulitermes virginicus (Banks) was described in 1907

as *Termes virginicus* from Falls Church and Chain Bridge, VA and Washington, DC (Banks & Snyder, 1920). Its range overlaps those of *R. flavipes* and *C. formosanus* but does not extend as far north as that of *R. flavipes*. From the southeast, it ranges westward to Houston, TX, northwestward to Missouri, and as far north as Long Island, NY (Weesner, 1970). Its alates are dark colored day-flyers, smaller than those of *R. flavipes*, and the ocelli are less than one ocellus diameter from the compound eye. In their typical mesic habitats, *R. virginicus* usually occupies lower, wetter sites, and *R. flavipes* occupies higher, drier sites (Howard *et al.*, 1982). Although its biology and range make it a likely pest, *R. virginicus* is generally considered less damaging than *R. flavipes*.

Beginning in the late 1940's, the United States termite control industry relied almost exclusively on the cyclodiene soil termiticides aldrin, dieldrin, and chlordane. These highly persistent chemicals were applied to soil under and around structural foundations. Termites encountering the termiticide are either killed outright, or, more likely, are repelled from the treated area. In spite of their efficacy, concern over the health risks associated with these products led to their removal from the market by 1988. New formulations of organophosphate and synthetic pyrethroid insecticides are now used as soil termiticides, but some doubt exists over their efficacy and environmental soundness. At

four gallons of emulsion per 10 linear feet of foundation, very large quantities of insecticide are routinely placed in close contact with human living space.

These concerns have inspired research into toxic bait technology. With this experimental technique, toxic, but palatable, baits are placed in areas of termite activity. Foragers eat the toxic food then feed it to their nestmates by trophallaxis. For a lethal dose to reach the nest, the bait toxicant must be non-repellent to foragers and sufficiently slow-acting to give them time to feed their nestmates. If the insecticide is thus delivered to the nest, it could conceivably kill the entire colony, rather than just repel its foragers as does a soil treatment. The insecticide doses are minute compared to conventional control. Field studies with toxic baits against termites have shown promising results in Canada (Esenther & Gray, 1968), Mississippi (Esenther & Beal, 1974), Connecticut (Beard, 1974), China (Gao, 1987), Australia (French, 1988), and Florida (Jones, 1989).

With the "blanketing" approach of repellent soil termiticides, knowing the subtleties of termite behaviors is less important. However, successful use of toxic baits will require sophisticated knowledge of termite feeding and foraging behaviors. For example, the design of baits requires knowledge of food preference, and successful placement of baits requires knowledge of termite foraging patterns.

This dissertation examines some feeding and foraging behaviors of *C. formosanus*, *R. flavipes*, and *R. virginicus*, three rhinotermitids with sympatric ranges in Louisiana. Where appropriate, the results were interpreted in light of toxic bait control. However, much information of basic value was gained. The first two chapters examine some ways termites allocate their foraging forces among food items. The next two chapters cover some factors affecting food choice. The fifth chapter describes differences in wood-excavating behavior of the three species, and the sixth chapter re-examines the suitability of an experimental dye that is widely used as a marker in termite foraging studies.

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Chapter 1

Variance in Feeding on Equivalent Wood Blocks by the Formosan Subterranean Termite in Laboratory Choice Tests

Sociobiology 13(3): 227-233

SUMMARY

In a laboratory choice feeding bioassay, I measured variance of feeding by groups of *Coptotermes formosanus* Shiraki on four equivalent wood blocks and tested whether group size affected variance of mg wood eaten at each block. In all cases, foraging was not random; termites concentrated on a few preferred blocks. Group size did not affect this pattern of non-randomness. These data are useful for designing choice tests, and recommended sample sizes for a simulated experiment are given.

INTRODUCTION

Termite food preference and the effects of attractants or repellents are often measured with choice tests (Amburgey & Smythe, 1977; Behr *et al.*, 1972; Carter *et al.*, 1983; Smythe & Carter, 1970). With this method, a container of termites is offered several items of interest (i. e., blocks of wood of different species), and attractiveness of the materials is measured by the amount of each one eaten. The null hypothesis is that termites feed equally on all items. It is useful, therefore, to have an idea of the inherent variability in termite feeding on multiple items that are made as similar as possible. In this study I measured variance of feeding by the Formosan subterranean termite (*Coptotermes formosanus* Shiraki) on four equivalent wood blocks and tested the effects of group size on variance of feeding. Such baseline information can be used to determine sample size for choice tests.

MATERIALS AND METHODS

Equipment. The same container unit design was used in two experiments (Fig. 1). Each unit consisted of a central chamber with sand matrix connected by four transparent PVC pipes of equal length to four smaller foraging chambers. Each foraging chamber contained a block of southern yellow pine (*Pinus* sp.) wood. Blocks were cut from boards bought at one lumber yard, were free of knots, and were moistened with the same amount of water within each experiment. Therefore, I

assumed all blocks were equally attractive to the termites. During each test, termites were free to feed on all blocks.

Termites. A corrugated fiberboard trap, similar to that described by La Fage *et al.* (1983), was used to collect termites from colonies in bald-cypress trees (*Taxodium distichum* [L.] Rich.) along the Calcasieu River near Lake Charles, Louisiana. Termites were held in the laboratory for one day in experiment 1 and for two days in experiment 2 before being used.

Experiment 1. This experiment measured variance of feeding by *C. formosanus* on four equivalent wood blocks. Eight units (Fig. 1) with 1000 termites each were established. Each central chamber received 461 g of acetone-washed sand and 55 ml of deionized water. Each foraging chamber received 30 g of sand and 12 ml of water. Termites from four colonies were used. On day 0, two groups of 1000 workers (undifferentiated larvae $\geq$ the third instar) were counted from each colony and each group was put into the central chamber of a unit. On day 1, one pre-weighed (oven dry mass) wood block was put in each foraging chamber. I delayed giving wood so the termites would tunnel into the sand matrix of the central chamber and not be prematurely attracted to a wood block. In earlier experiments where the termite "nest" was separate from a food source, termites would often abandon the "nest" and occupy the "foraging" chamber. All units were kept in one bioclimatic chamber at 29 ± 1.5° C. On days 67 and 68,

the units were dismantled. Wood blocks were cleaned, oven dried, and re-weighed to determine the amount of each one eaten. The standard deviation of mg wood eaten at each block/day was calculated for each unit. Rate (mg/day) was used because units were not all dismantled on the same day.

Experiment 2. This experiment tested whether group size affected variance of mg wood eaten at each block. A randomized design blocked on colony was used with three colonies, four group sizes (125, 250, 500, and 1000 termites), and two replicates per colony X group size (24 experimental units). The amount of matrix in the central chamber was proportional to group size. Central chambers of units with 125 termites received 62.5 g of sand and 8.1 ml of deionized water; 250 termites received 125 g and 16.3 ml; 500 termites received 250 g and 32.5 ml, and 1000 termites received 500 g and 65 ml. Each foraging chamber received 18.5 g and 9 ml. On day 0, workers were counted, and each group was put in the central chamber of a unit. On day 3, a wood block was put in each foraging chamber. All 24 units were kept in one room at 28 ± 1.5° C. Each day during days 4-7, I inspected each unit and recorded which foraging chambers had termites or evidence of termite visitation, such as sand foraging tunnels in the clear PVC pipes. On days 61 and 62, units were dismantled and percentage survival for each unit was measured. Wood was processed as in experiment 1. The coefficient of variation (CV) for mg wood eaten at each block was calculated for each

unit, allowing me to compare variance in wood feeding of different group sizes despite their large differences in total wood consumption.

Data Analysis. Analysis of variance, blocking on colony, was used to compare mean CV for mg wood eaten of the different groups sizes. Group size X colony interaction was the error term. Arcsin transformation was used on survival percentage data. A regression analysis for each group size was used to determine the correlation of mg wood eaten at each block with the number of workers in that chamber when the experiment was dismantled.

Sample Size Calculation. I calculated a recommended sample size for choice tests with 1000 termites using the noncentrality parameter described by Neter and Wasserman (1974) and the data for mg eaten at each block for the 1000 group size in the second experiment (6 units) (values used: σ^2 = 780203 [variance for mg eaten at each block in the 1000 group], α = 0.05, power = 0.90 and 0.95, and $\Sigma\tau^2$ = 2495486. $\Sigma\tau^2$ was found by ranking blocks of each unit by mg eaten then using the means of the highest to lowest blocks for all units. These four means were used as "treatment" means [Table 3]). This calculated sample size is the N needed per treatment to find significant differences with the treatment deviations, α level, and number of treatments chosen.

RESULTS AND DISCUSSION

Experiment 1. Mean standard deviation of mg wood eaten at each block/day for eight units was 10.01 (Table 1). Termites did not feed equally at four equivalent blocks but fed mostly at a few preferred blocks.

Experiment 2. Again, termites did not feed equally at four blocks but had preferred blocks. Furthermore, this pattern of non-randomness did not change with group size; the coefficients of variation for mg eaten at each block were not different for any group size ($P = 0.4025$, Tables 1 and 2). Smaller groups did not partition their foraging force more or less randomly than did larger groups. Survival was not different among group sizes ($P = 0.5301$, Tables 1 and 2). In 16/24 units (66.7%), the most heavily damaged block was either the first block, or one of the first blocks visited during days 4-7. Likewise, in 16/24 units, the least damaged block was either the last visited during days 4-7 or apparently was visited after day 7. Termites seemed to concentrate on the blocks they first visited. There were significant positive correlations between mg wood eaten at each block and number of workers in that chamber when the experiment was dismantled. These correlations were: $R = 0.88$ ($P = 0.0001$) for the 125 group, 0.75 ($P = 0.0001$) for the 250 group, 0.48 ($P = 0.0167$) for the 500 group, and 0.72 ($P = 0.0001$) for the 1000 group. While dismantling the experiment, I rarely found blocks that were both heavily damaged but without termites. These results

suggest that within the 9-10 week period, termites concentrated on selected blocks and rarely moved to new ones. However, it is likely that termites would have fed equally at all blocks if they had had enough time, but my results suggest they would do so sequentially.

In a field study, Su *et al.* (1984) concluded that workers of *C. formosanus* select randomly among several available foraging sites. They dye-marked workers, re-released them, recorded their frequency among several trapping stations, and found that dyed workers occurred with equal frequency at all stations. Whereas Su *et al.* measured the frequency of dyed workers, I measured actual wood feeding at different sites. It is possible that termites randomly visited all chambers in my study, but actual feeding was not random.

Sample Size for Choice Tests. These data demonstrate the inherent variation in termite feeding when termites are given multiple, equivalent food items. Baseline data such as these are useful for estimating sample size in choice tests. For the four treatment deviations (mg wood eaten) given in Table 3 and $\alpha = 0.05$, six experimental units per treatment are needed for power = 0.90. For power = 0.95, seven experimental units are needed.

Conclusions. Termite feeding on equivalent blocks was not random, even though blocks were as similar as possible. I did not identify factors affecting termite preference among apparently equivalent wood blocks. It seems, however, that

once termites chose a particular block, they foraged on it to the exclusion of others. The development of wood excavations, tunnels, and pheromonal trails in a particular block doubtless encouraged termites to return to it.

TABLE 1. Mean standard deviation (SD) of mg wood eaten at each block/day and ANOVA means for coefficients of variation (CV) for mg wood eaten at each block and for percentage survival. Means for CV and survival were not different. Termites were given four equivalent wood blocks.

Experiment	Group Size	N	(SD) (mg/day)	CV	Percentage Survival
1	1000	8	10.01	.	.
2	125	6	3.96	52.8	60.9
2	250	6	6.83	73.5	68.9
2	500	6	11.50	74.0	71.5
2	1000	6	16.08	61.5	70.6

TABLE 2. ANOVA table for mean coefficient of variation (CV) for mg wood eaten at each block and percentage survival for experiment 2. Termites were given 4 equivalent wood blocks. Group size X colony interaction is the error term.

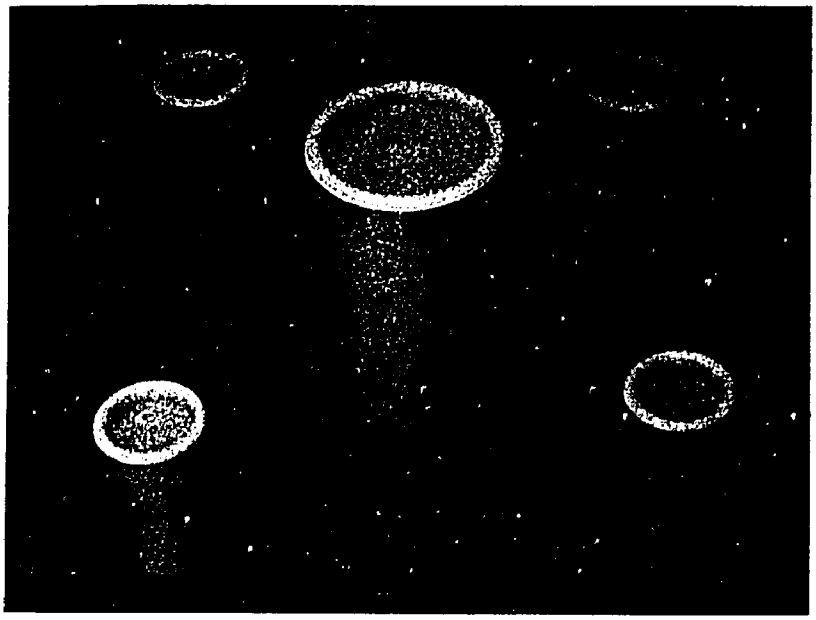
Variable	Source	DF	MS	F	P > F
CV	group size	3	628.7	1.15	0.4025
	colony	2	1215.9	2.22	0.1893
	group X colony	6	546.6	5.82	0.0048
Survival	group size	3	0.018	0.82	0.5301
	colony	2	0.031	1.37	0.3230
	group X colony	6	0.022	0.76	0.6165

TABLE 3. Simulated treatment deviations derived from data for 1000 group size in experiment 2 used to estimate sample size needed to show these means as different.

	Treatment Means (mg wood eaten)				Grand
	1	2	3	4	Mean
	544	1158	1931	2639	1568
Deviations	-1024	-410	363	1071	

FIGURE 1

Polyvinyl chloride (PVC) apparatus used to measure variance of termite feeding on equivalent wood blocks. Central chamber (13.5 cm tall by 7.6 cm ID) was connected by clear PVC pipes (9.8 cm long by 1.2 cm ID) to four smaller foraging chambers (7.7 cm tall by 3.9 cm ID). Each small chamber contained a block of southern yellow pine (*Pinus* sp.) ca. 5.0 by 2.5 by 1.5 cm. The tops and bottoms of each chamber were plastic friction caps.



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Chapter 2

Foraging Tenacity of *Reticulitermes flavipes* (Kollar) and *Coptotermes formosanus* Shiraki (Isoptera: Rhinotermitidae)

Sociobiology 16(2): 183-189

SUMMARY

Termites were placed in laboratory foraging arenas in which successive, equi-distant baits were attached to a "nest". Foraging tenacity was measured as the percentage mass of a bait eaten by termites before the insects began foraging on the next bait; this parameter was compared for *Reticulitermes flavipes* (Kollar) and *Coptotermes formosanus* Shiraki. On average, *C. formosanus* consumed a greater percentage of a wood block before moving (10.3%) than did *R. flavipes* (4.2%), and termites were most tenacious at the first bait outside the nest and became less tenacious with distance. Depletion of discovered food may be a stimulus for termites to resume exploratory foraging, and this "depletion threshold" varies with species. Since termites exploit foodstuffs with low nutritive value, tenacity at discovered food may be energetically cost-effective.

INTRODUCTION

Subterranean termites appear to choose randomly among available food items (Su *et al.*, 1984; Jones *et al.*, 1987). However, once these insects discover a favorable food site, they forage there tenaciously (Delaplane & La Fage, 1987 [Chapter 1]; Jones *et al.*, 1987), even if initially favorable conditions change (Delaplane & La Fage, 1989 [Chapter 3]). In this study, I sought to quantify and compare foraging tenacity of two rhinotermitids by measuring the percentage dry mass of a wood bait eaten by termites before the insects voluntarily moved to another bait.

MATERIALS AND METHODS

Termites. Workers (undifferentiated larvae $\geq$ the third instar) of *Reticulitermes flavipes* (Kollar) from three colonies were collected in fallen pine (*Pinus* sp.) logs at the Harrison Experimental Forest, USDA Forest Service, Southern Forest Experiment Station, near Gulfport, Mississippi. Workers of *Coptotermes formosanus* Shiraki were collected from seven colonies in baldcypress trees (*Taxodium distichum* [L.] Rich.) growing in water along the Calcasieu River near Lake Charles, Louisiana.

Apparatus. Polyvinyl chloride pipe was used to make laboratory foraging arenas. Each arena consisted of five stations of vertical pipe (each 14 cm tall by 4 cm ID) connected to each other successively with sections of

horizontal transparent pipe (10 cm long by 1.2 cm ID). The horizontal connecting pipes were inserted in holes drilled in the stations 1.5 cm from the bottom. The tops and bottoms of the stations were plastic friction caps. Distance between stations was 13 cm, center to center. The first station of each arena was designated the "nest" and was provided with matrix, one block of wood, and termites; the remaining stations were designated as baits 1 through 4, consecutively, and were each provided with one block of wood. In this manner, wood blocks were available to termites at any of five distances from the nest (0, 13, 26, 39, and 52 cm).

Reticulitermes flavipes Assay. I determined foraging tenacity of *R. flavipes* at successive baits. First, the nest station of each arena was removed and the transparent pipe leading from it was plugged. Into each nest station were placed 11 g oven dried vermiculite (heat-expanded mica substrate), 25 g deionized water, one oven dried wood (*Pinus* sp.) temporary feeding block about 1.8 by 1.8 by 1.8 cm, and 1000 workers. These conditions provided the optimum moisture and density conditions for *Reticulitermes* as derived from the data of Lenz *et al.* (1987). There were eight nest stations for colony 1 and four each for colonies 2 and 3 for a total of 16. All nest stations were kept in a bioclimatic chamber at 27 ± 1° C and 90 ± 5% RH for seven days. This gave termites time to tunnel in the matrix of the nest station; preliminary work suggested that termites will move into bait

stations and abandon the nest if they are given a complete foraging arena at once. After the 7-day "settling-in" period, the transparent pipe from each nest station was unplugged, and four successive bait stations were attached. Inside each bait station was one pre-weighed, oven dried block of wood (*Pinus* sp.). The temporary feeding block in the nest was replaced with one of the new blocks. All 16 complete arenas were returned to the bioclimatic chamber (day = 0).

Starting on day 0 and continuing through day 27, regular visual observations were made to record the time when termites began foraging at each bait. Altogether, 28 observations were made at roughly 24-h intervals.

On days 27 and 28, the arenas were dismantled. Each wood block was brushed clean, oven dried, and re-weighed to determine feeding rate (mg wood eaten per day) relative to the time termites began feeding on the block. I assumed that termites began feeding on blocks in the nest stations on day 0. With the following data for each block - initial mass, the day on which termites began feeding on it, and feeding rate - I calculated the percentage dry mass of a block that termites ate before they began feeding on the next block (foraging tenacity). Because no bait followed bait 4 (52 cm), this parameter could be calculated only for the nest blocks and for baits 1 through 3. I assumed in my calculations that feeding rate was constant over time; Su & La Fage (1984) showed that feeding by *C. formosanus* was constant in trials of up to 42

days in length.

Coptotermes formosanus Assay. Foraging tenacity of *C. formosanus* at successive baits was tested similarly as described above. Nest stations received 25 g dried vermiculite, 56 g deionized water, one temporary feeding block, and 1000 workers, thus providing the optimum conditions for *C. formosanus* (Lenz *et al.*, 1987). There were at least two arenas for each of the seven colonies for a total of 16. Visual observations began on day 0 and continued through day 53 (29 observations total) when the experiment was dismantled. Even though feeding rates of *C. formosanus* become more erratic after 42 days (Su & La Fage, 1984), I felt it was necessary to prolong the experiment because termites were still moving to new baits.

Analysis. I tested the effects of species and distance from the nest on foraging tenacity. A factorial design analysis of variance, blocked on colony source of termites and recognizing species and distance as main effects was used. Colony effects nested within main effects interaction was the error term for testing both the main effects and their interaction with each other. Least significant difference (LSD) mean separation was used to identify treatment differences, and $\alpha \leq 0.05$ was the accepted level of significance. One *C. formosanus* arena was removed from the analysis because a large number of termites had escaped from it.

RESULTS AND DISCUSSION

Foraging tenacity was affected by species ($P = 0.02$) and distance from the nest ($P = 0.0008$). On average, *C. formosanus* consumed a greater percentage of a wood block before moving (10.3%) than did *R. flavipes* (4.2%), and termites were most tenacious at the first bait outside the nest and became less tenacious with distance (Table 1). However, main effects interactions occurred ($P = 0.0001$), largely from the unresponsiveness of *R. flavipes* to distance.

The greater tenacity shown by *C. formosanus* was unexpected, owing to the reputation of this species for voracity (Smythe & Carter, 1970) and for vigorous tubing in laboratory cultures (Su & Tamashiro, 1987). *Coptotermes formosanus* typically feeds at higher rates than does *Reticulitermes* spp. (Smythe & Carter, 1970). My data suggest that one mechanism for higher feeding rates may be a greater tenacity of *C. formosanus* at discovered food sites.

The design of the arenas imposed obvious constraints on foraging options. However, my parameter of tenacity required directionality of foraging and precise data on time of termite visitation. In an "open" arena, termites could conceivably attack several baits at once, preventing me from measuring tenacity for any single bait.

Depletion of discovered food may be a stimulus for termites to resume exploratory foraging, and this "depletion threshold" varies with species. This may promote niche

separation and competition avoidance in termite communities.

Termite foraging at profitable food sites can be intense. For example, when *C. formosanus* is offered bait stations with X or 2X amounts of a preferred food (*Pinus* sp.), the termites allocate almost twice as many foragers to the 2X stations (Waller & La Fage, 1987a). Termites exploit foodstuffs with relatively low nutritive value (Waller & La Fage, 1987b). Furthermore, the "giving-up time" (Krebs *et al.*, 1974) of animals foraging at a patch varies inversely with the richness of the habitat (Krebs *et al.*, 1974; Pyke *et al.*, 1977). In the limited nutritive regimes associated with termites, the energetic costs of foraging activities, such as construction of protective soil tubing (MacKay *et al.*, 1985), may be important regulators of foraging patterns. Therefore, tenacity of termites at discovered food may be energetically cost-effective.

TABLE 1. Foraging tenacity[1] of termites as affected by species and distance from the nest. LSD mean separations were done separately for the distance by species interactions (8 means), for species means (2 means), and for distance means (4 means); within these groupings, means followed by the same letter are not different ($\alpha \leq 0.05$).

	Distance (cm)				
Species	0	13	26	39	Species Means
R. flavipes	2.9c	5.2bc	4.3bc	5.2bc	4.2b
C. formosanus	1.7c	20.3a	10.9b	6.6bc	10.3a
Distance Means	2.3c	13.9a	8.1b	5.9bc	

[1]In an arena of successive baits, the percentage dry mass of a wood bait eaten before termites began foraging on the next bait.

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Chapter 3

Preference for Moist Wood by the Formosan Subterranean Termite (Isoptera: Rhinotermitidae)

J. Econ. Entomol. 82(1): 95-100

SUMMARY

In a laboratory choice feeding test, groups of *Coptotermes formosanus* Shiraki were offered wood blocks that differed in initial moisture content. Wood feeding rate, number of workers, and number of soldiers were highest in the high moisture treatment. In higher moisture blocks, damage by termites was associated with loss of block moisture, but in lower moisture blocks damage was associated with gain of moisture. Even though block moisture contents changed, termites determined their preferred wood blocks early when moisture contents were more discrete, then they continued to prefer those blocks. Changes in moisture were probably due to blocks equilibrating to ambient relative humidity of the containers, but termites enhanced this process, perhaps by actively relocating water. My data imply that damp wood in buildings is especially vulnerable to *C. formosanus* and that bait blocks for remedial control of this pest should have high moisture content.

INTRODUCTION

Because the workers, or pseudergates, of most termite species are only lightly sclerotized, these insects are highly vulnerable to desiccation. Consequently, water relations govern many facets of termite biology. Species distribution (Strickland, 1950; Haverty & Nutting, 1976), termite density in soil (Ueckert *et al.*, 1976), and timing of alate flights (Nutting, 1969) are at least partly affected by environmental moisture. Foraging by the desert termites *Heterotermes aureus* (Snyder) (Haverty *et al.*, 1974) and *Gnathamitermes perplexus* (Banks) (La Fage *et al.*, 1976) increases in response to elevated soil moisture after rain. The African species *Macrotermes natalensis* (Haviland) constructs its nests so that humidity, ventilation, and temperature are closely controlled (Lüscher, 1961).

There has been much interest in determining the desiccation tolerances and humidity preferences of different termite species (Collins, 1969; Minnick *et al.*, 1973; Steward, 1982). However, there has been less research on termite wood moisture preference. Becker (1965) showed that *Heterotermes indicola* (Wasmann) and *Reticulitermes lucifugus* (Rossi) prefer moist wood over drier wood only when no wet soil matrix is provided. Hrdý & Zelený (1967) found only a slight preference for moist wood with another rhinotermitid, *Prorhinotermes simplex* (Hagen), a species that often lives in wood rather than in subterranean nests. In both these choice studies,

wood blocks of different moisture content were placed immediately next to each other - a situation I believe may obscure the discrete effects of any given treatment and jeopardize the independence of observations.

In recent years, the imported rhinotermitid *Coptotermes formosanus* Shiraki has become a serious urban pest in parts of the southeast United States. This termite builds extensive carton nests inside buildings near sources of water such as condensation on plumbing and effectively bypasses the soil contact requirement of most other subterranean termites. Consequently, research on wood moisture preference of this species is especially timely. In this paper, I present the results of a choice test with *C. formosanus* in an apparatus in which wood blocks were separated from each other. Because wood moisture changed dramatically during the choice test, I designed two experiments in termite-free conditions to clarify the reasons for this change.

MATERIALS AND METHODS

Apparatus. Polyvinyl chloride (PVC) termite containers (units) used in all tests were described by Delaplane & La Fage (1987 [Chapter 1]). Each unit consisted of a central chamber (containing moistened sand matrix) and four smaller removable foraging chambers connected at right angles to the central chamber with transparent PVC pipe. Each foraging chamber was provided with one block of wood. With this

apparatus, wood blocks of different treatments were separated.

Choice test of wood moisture preference. Preference of *C. formosanus* among wood blocks with different moisture content was tested in a randomized design blocked on colony source of termites. Termites were collected from six colonies along the Calcasieu River near Lake Charles, Louisiana, then held in the laboratory for one day before being used.

Wood blocks were southern yellow pine (*Pinus* sp.), free of knots, cut to ca. 3.4 cm^3, and oven dried before treatment. Blocks were treated by individually soaking them in deionized water for different lengths of time and calculating percentage water uptake on a dry mass basis. "High" moisture blocks (H) (96.3 ± 1.6% initial moisture content) soaked for six days and were removed from water shortly before the start of the choice test (on day three, see below). "Medium" moisture blocks (M) (53.0 ± 1.2%) soaked for 30 minutes, were drained, then kept covered for three d until day three. "Low" blocks (L) (13.9 ± 0.4%) were dipped in water for about one second on day three. "Control" blocks (C) (3.1 ± 0.2%) were removed from the oven and kept covered for three d until day three, allowing some atmospheric moisture to be absorbed. All moisture determinations were made on day three shortly before the choice test started.

I established 17 units (6 colonies by 3 units per colony minus 1 unit due to lack of termites). To each central chamber, I added 260 g acetone-washed sand, 32 ml deionized

water, 1000 workers (undifferentiated larvae ≥ the third instar), and a temporary wood feeding block (removed on day three). These conditions approached the optimum number of termites per ml matrix density of 6.4 for this species as derived from the data of Lenz *et al.* (1987). Central chambers were kept in a bioclimatic chamber at 28.1 ± 1.2° C, 98 ± 1.0% relative humidity and constant darkness. I delayed attaching the foraging chambers to the central chamber until day three to give termites time to tunnel in the sand of the central chamber. On day three, each foraging chamber of each unit randomly received a wood block of one of the four initial moisture contents.

Intact units were maintained in the bioclimatic chamber from day 3 to 17, giving the test blocks a 14 day exposure to the termites. No water was added to the units during the test. On days 4, 5, 6, 10, 11 and 12, the transparent pipes connecting the foraging chambers to the central chamber were inspected visually for evidence of termite activity. Units were dismantled on day 17. Foraging chambers and their connecting pipes were removed and plugged as quickly as possible to trap the termites. Wood blocks were cleaned, weighed, oven dried, and re-weighed to determine changes in percentage moisture since the beginning of the experiment (ΔM) and wood feeding rate (mg eaten/d). Numbers of workers and soldiers in each foraging chamber were counted.

Analysis of variance, blocked on colony, with least

significant difference (LSD) mean separation (Proc GLM, SAS Institute, 1985, pp. 183-260) was used to compare wood feeding rate, number of workers, and number of soldiers among treatments. Treatment X colony interaction was the error term and was never significant. Regression analyses with linear and quadratic terms were used to test the relationship of ΔM with mg wood removed from the block (Proc REG, SAS Institute, 1985, pp. 269-336). Average ΔM for each treatment was tested against zero with a *t* test (Proc Means, SAS Institute, 1985, pp. 351-352).

First termite-free test, changes in undamaged wood. During the 14 day choice test with termites, moisture contents of wood blocks of all treatments tended to converge. This raised the possibility that termites, or their excavations, affected the moisture content of wood. I conducted an experiment to determine whether moisture of undamaged wood changes in termite-free conditions. I established 14 units exactly as before (except that foraging chambers were attached from the onset) but did not add termites. Blocks were treated in water exactly as described before. Each foraging chamber of each unit randomly received an undamaged wood block of one of four initial moisture contents: H (106.4 ± 2.0%), M (71.4 ± 0.9%), L (8.9 ± 0.8%), and C (4.5 ± 0.1%). All units were kept in the same bioclimatic chamber as before at 28.4 ± 0.4° C, 98.1 ± 0.4% relative humidity, and constant darkness. Daily, at nearly 24 h intervals, a randomly chosen unit was

dismantled and each block weighed to calculate ΔM. Empty units were returned to the bioclimatic chamber so that air currents in the chamber would not be altered.

Average ΔM for each treatment was tested against zero with a *t* test. The relationship of ΔM with time (day) was tested by regression analyses with linear and quadratic terms. I tested the hypothesis that the difference in ΔM between a treatment in the termite choice test and the same treatment in the termite-free test was zero. From each observation for ΔM in the choice test (only available for the 14th day of termite exposure), an equivalent value for ΔM from the same treatment in the first termite-free test was subtracted. Equivalent values from the termite-free test were the mean ΔM over 14 days for those treatments without significant slopes (H and M) and the predicted value for ΔM at day 14 for those treatments with significant slopes (C and L). For each treatment, the mean of these differences was tested against zero with a *t* test.

Second termite-free test, changes in damaged wood. In the choice test with termites, wood blocks of different moisture content sustained variable degrees of termite damage. Therefore, it is possible that the convergence of moisture contents was an artifact of block damage. I conducted an experiment to determine whether moisture of damaged wood changes in termite-free conditions. I set up 14 units as in the first termite-free test. Termite-damaged blocks were

collected and scored into two levels of damage: "high" (D) (extensive boring through block) and "low" (d) (damage limited to surface abrasion). Blocks of each damage level were, in turn, moistened to either "high" (M) or "low" (m) moisture content. This gave four block treatments: DM (83.4 ± 7.8% initial moisture content), dM (67.6 ± 5.0%), Dm (23.9 ± 5.6%), and dm (20.9 ± 5.7%). Each foraging chamber of each unit randomly received one of these treatments. All units were kept in the same bioclimatic chamber as before at 28.6 ± 0.2° C, 98.2 ± 0.4% relative humidity and constant darkness. Daily, a randomly chosen unit was dismantled, and ΔM were determined as before.

Average ΔM for each treatment was tested against zero as before. The relationship of ΔM with time was tested with regression analyses. ΔM of blocks from the H treatment in the termite choice test was compared with change of moisture of DM blocks from this termite-free test. Likewise, blocks from the L treatment in the choice test were compared with dm blocks. These analyses were the same as described in the previous section. Equivalent values for ΔM from the second termite-free test were the predicted values for ΔM at day 14 for the DM treatment and the mean ΔM for the dm treatment.

RESULTS AND DISCUSSION

Choice test of wood moisture preference. There were differences among treatments for wood feeding rate ($F = 29.12$;

df = 3,15; P = 0.0001, Table 1). Feeding rate was highest at the high (H) wood blocks. There were no colony effects (F = 1.0; df = 5,15; P = 0.4527).

There were differences among treatments for number of workers in the foraging chamber at the end of the experiment (F = 5.73; df = 3,15; P = 0.0081, Table 1), but there were no colony effects (F = 0.29; df = 5,15; P = 0.9104). Number of soldiers in the foraging chamber also differed among treatments (F = 8.14; df = 3,15; P = 0.0019, Table 1), and the pattern was similar to that for number of workers. Again, there were no colony effects (F = 2.16; df = 5,15; P = 0.1142). Soldiers were not added to the units but had molted from workers during the experiment.

Workers of C. *formosanus* clearly preferred wood with the highest initial moisture content. Wood feeding rate, number of workers, and number of soldiers were nearly double in the H blocks over any other treatment. Furthermore, these differences in feeding rate were apparently unaffected by the order in which foraging chambers were first visited, as Delaplane & La Fage (1987 [Chapter 1]) had found in a study using this same container design with equivalent wood blocks. In the present study, vigorous termite activity was found after 24 h at wood blocks of all treatments except medium (M); after 48 h there was also strong activity at M blocks. Termites discovered blocks of all treatments fairly early, even though subsequent feeding rates differed.

During the 14 day test, percentage moisture of wood blocks tended to converge; high moisture blocks lost moisture, and low moisture blocks gained moisture. Changes in percentage moisture (ΔM) were always different from zero and were -43.8% (t = -11.91; df = 16; P = 0.0001) for the H treatment, -6.9% (t = -4.82; df = 16; P = 0.0002) for the M treatment, 15.6% (t = 22.38; df = 16; P = 0.0001) for the low (L) treatment, and 24.4% (t = 23.46; df = 16; P = 0.0001) for the control (C) treatment. Ending moisture content of M blocks (46.1 ± 5.7%) was not much less than that of H blocks (52.4 ± 15.0%), yet feeding rate at M blocks was significantly lower. These data again demonstrate the overwhelming preference for blocks with the highest initial moisture. Termites apparently determined their preferred blocks early when moisture contents were more discrete, and thereafter they were little affected by changes in moisture. There were clear relationships between ΔM and mg wood removed from the block, but the patterns were different between the higher moisture and lower moisture treatments. The regression of ΔM on mg wood removed was described by a model (r = 0.80) with a linear coefficient (slope =- 0.04 ± 0.009) for the H treatment, a model (r = 0.77) with a linear coefficient (slope = -0.02 ± 0.005) for the M treatment, a model r = 0.76) with a linear coefficient (slope = 0.03 ± 0.007) for the L treatment, and a model (r = 0.80) with linear (slope = 0.09 ± 0.02) and quadratic (slope = -0.0001 ± 0.00003) coefficients for the C

treatment. Generally, as higher moisture blocks were fed upon and their surface areas enlarged, they lost moisture, but as lower moisture blocks were damaged, they gained moisture. This suggests that blocks were equilibrating to the ambient relative humidity of the containers and that increases in surface area enhanced this process.

Reticulitermes spp. are the most important termite pests of North America. Becker (1965) found that a congener of North American *Reticulitermes* does not discriminate between blocks of different moisture content when the termites are given wet matrix. In my study, *C. formosanus* had access to wet matrix and still preferred moist wood. This implies that moist wood in buildings is especially vulnerable to damage by subterranean colonies of *C. formosanus*. Hrdý & Zelený (1967) found only a marginal preference for moist wood with another rhinotermitid whose nests, as with *C. formosanus*, are not limited to the soil. In considering all three studies, it seems that the Rhinotermitidae vary in wood moisture preference and in their use of soil moisture as a regulator of food choice.

With the demise of conventional cyclodiene termiticides, bait block methods of remedial treatment are appealing alternatives (Beard, 1974). Bait blocks are sometimes decayed with the fungus *Gloeophyllum trabeum* (Pers. ex Fr.) Murr. to make them more attractive to termites (Esenther & Beal, 1979). Bait blocks for control of *C. formosanus* should probably be

kept moist to increase their attractiveness.

There are many likely reasons for the preference for moist wood by *C. formosanus*. Behr *et al.* (1972) showed that termite feeding was negatively correlated with wood hardness. In my study, wood fibers in the high moisture blocks were probably softened and, consequently, easier to masticate. Mishra & Sen-Sarma (1979) found that the coefficient of digestibility increases for drywood termites with a rise in atmospheric relative humidity and that this is often associated with increased feeding. The movement of food through the termite gut increases at high relative humidity (Kovoor, 1967), and this can regulate food intake (Mishra & Sen-Sarma, 1979). In my study, high moisture blocks may have provided a humid microenvironment in which similar phenomena occurred.

First termite-free test, change in undamaged wood. In termite-free conditions, average ΔM of undamaged wood were always different from zero and were -2.35% (t = -2.94; df = 13; P = 0.0115) for the H treatment, -4.97% (t = -9.60; df = 13; P = 0.0001) for the M treatment, 3.86% (t = 4.21; df = 13; P = 0.0010) for the L treatment, and 7.40% (t = 8.60; df = 13; P = 0.0001) for the C treatment. The regression of ΔM on time for the L and C treatments were described by models with linear and quadratic coefficients, and the slopes for ΔM against time for H and M blocks were zero (Fig. 1).

In termite-free conditions, a slight convergence of

moisture contents occurred, but, except for the M treatment, it was dramatically less than in the termite choice test (Fig. 1). There were differences in ΔM between the two experiments with the H (t = -11.27), L (t = 15.63) and C (t = 15.00) treatments (df = 16; P = 0.0001 each). Compared with the termite choice test, in termite-free conditions H blocks lost less moisture, and L and C blocks gained less moisture.

Second termite-free test, changes in damaged wood. In termite-free conditions, average ΔM of blocks of all four damage : moisture combinations were always different from zero and were 4.52% (t = 3.06; df = 13; P = 0.0091) for the DM treatment, 3.89% (t = 5.38; df = 13; P = 0.0001) for the dM treatment, 2.31% (t = 3.35; df = 13; P = 0.0053) for the Dm treatment, and 2.72% (t = 4.98; df = 13; P = 0.0003) for the dm treatment. There was a linear decrease in ΔM with time in the DM treatment; these blocks tended to gain moisture, but the amount of gain decreased with time to negative values (Fig. 2). This pattern in the DM treatment was clearly different from the large loss of moisture in the H blocks of the choice test, and ΔM between these two treatments differed (t = -11.55; df = 16; P = 0.0001). The slopes were zero for all other treatments in the second termite-free test. Blocks of the L treatment of the choice test gained more moisture than did blocks of the dm treatment (t = 18.48; df = 16; P = 0.0001).

Summary. In a choice feeding test, groups of *C.*

formosanus preferred wood blocks with the highest initial moisture content. Because blocks of different treatments were separated, all observations were independent. In higher moisture blocks, wood removal by termites was generally accompanied by loss of block moisture, but in lower moisture blocks, wood removal was accompanied by gain of moisture. It was uncertain whether this was simply block equilibration to ambient relative humidity or a termite-mediated event. To study this phenomenon, I measured change of moisture of both undamaged and termite-damaged wood blocks in termite-free containers then tested whether changes of moisture under these conditions were the same as those of comparable treatments in the termite choice test. These "across-experiment" tests did not compare perfectly equivalent conditions. For example, wood damage occurred gradually in the choice test but was present from the onset in the second termite-free experiment. Nevertheless, the termite-free experiments demonstrated changes in wood moisture that could be expected in hypothetical termite-free conditions.

High moisture blocks in the choice test lost more moisture than did either undamaged or damaged high moisture blocks in termite-free conditions. Furthermore, low moisture blocks of the choice test gained more moisture than did either undamaged or damaged low moisture blocks in termite-free conditions. In termite-free containers, undamaged wood seemed to equilibrate toward ambient relative humidity, and damaged

wood, on the average, tended to gain moisture. It is puzzling why highly damaged, moist blocks (DM) of the second termite-free test gained so much moisture at first. They too, however, showed a trend toward equilibration. One could argue that the loss of moisture in high moisture blocks of the choice test was from a disproportionate removal of the water-absorbent and termite-favored early wood, but this would not explain the simultaneous gain in the lower moisture blocks. I believe that much of the moisture convergence in the choice test was from block equilibration, but there is indirect evidence that termites enhanced the process, perhaps by actively relocating water. Imbibition of free water is known in alates of *Hodotermes mossambicus* (Hagen) (Hewitt *et al.*, 1971) and in workers of *Macrotermes michaelseni* Sjöstedt (Sieber & Leuthold, 1981). If relocation of free water by rhinotermitids occurs, more direct evidence is needed to prove it.

TABLE 1. Preference of *C. formosanus* for wood blocks differing in initial moisture content[1]

Initial Moisture	Feeding Rate (mg/day)	No. Workers	No. Soldiers
high	50.3 ± 19.7 a	257.4 ± 206.0 a	5.1 ± 6.3 a
medium	27.5 ± 13.9 b	112.6 ± 108.6 b	1.0 ± 2.1 b
low	18.3 ± 5.0 c	129.3 ± 128.3 b	2.3 ± 4.3 b
control	20.1 ± 8.4 bc	116.6 ± 107.8 b	1.5 ± 2.4 b

[1]Column means (± standard deviations) with different letters are significantly different ($P \leq 0.05$; LSD mean separation [SAS Institute 1985]).

FIGURE 1

Change in percentage moisture (ΔM) of undamaged wood blocks kept in termite-free containers. Blocks were initially dampened to either high (H), medium (M), or low (L) moisture content or were allowed only to absorb atmospheric moisture (control, C). On each of 14 days, a unit was dismantled, and its blocks were measured. Significant slopes only occurred with the L and C blocks. For comparison, average ΔM in the choice test with termites was -43.8% in the H treatment, -6.9% in the M treatment, 15.6% in the L treatment, and 24.4% in the C treatment.

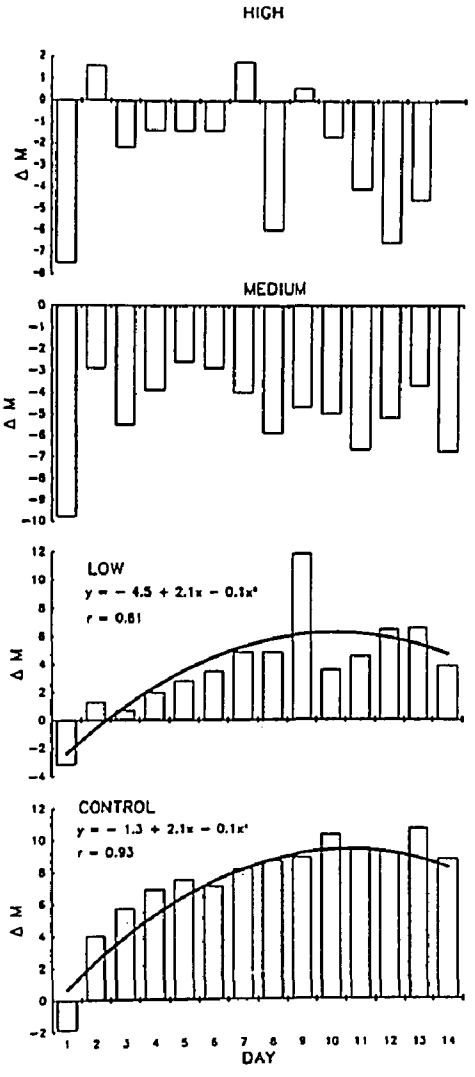
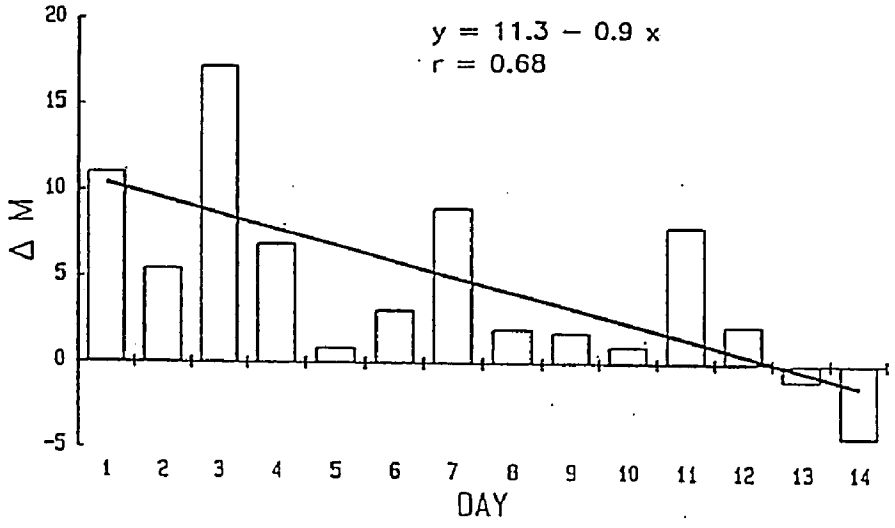

HIGH
MEDIUM
LOW
y = − 4.5 + 2.1x − 0.1x²
r = 0.81
CONTROL
y = − 1.3 + 2.1x − 0.1x²
r = 0.93
Δ M
DAY

FIGURE 2

Change in percentage moisture (ΔM) of wood blocks kept in termite-free containers and sampled as described in Figure 1. Blocks had sustained high previous termite damage and were dampened to 83.4 ± 7.8% initial moisture content.



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Chapter 4

Preference of the Formosan Subterranean Termite (Isoptera: Rhinotermitidae) for Wood Damaged by Conspecifics

J. Econ. Entomol. 82(5): 1363-1366

SUMMARY

In a laboratory choice feeding test, groups of termites from five colonies of *Coptotermes formosanus* Shiraki were presented with wood blocks that had been previously damaged: 1) by nestmates, 2) by conspecifics from another colony, 3) by another termite species, *Reticulitermes virginicus* (Banks), and 4) no damage. *Coptotermes formosanus* preferred wood previously damaged by conspecifics, regardless of colony origin, over wood damaged by *R. virginicus* or undamaged wood. Additionally, they preferred wood damaged by *R. virginicus* over undamaged wood. Covariate analyses and trail-following assays suggested that the results were almost entirely explained by thigmotaxic cues on the surface of damaged wood blocks rather than on pheromonal cues deposited on the wood.

INTRODUCTION

One alternative to persistent soil termiticides is the use of baits impregnated with slow acting toxicants. Baits are placed in areas of termite activity where the toxicant is ingested by foragers then taken to the nest and distributed by trophallaxis. Toxic baits can provide both preventive and remedial control of termites (Esenther & Beal, 1979) with a fraction of the insecticide rate used in conventional soil treatment.

Although toxic baits may kill entire colonies, they provide no spatially continuous insecticide barrier, and the resulting "termite-free" zone is open to reinfestation. Furthermore, wood moderately damaged by termites before treatment may be attractive to reinfesting termites. In this study, I tested the preference of *Coptotermes formosanus* Shiraki for wood previously damaged by termites. Such information could be useful in understanding termite food choice and in designing a toxic bait strategy.

MATERIALS AND METHODS

I tested the preference of *C. formosanus* for wood blocks that had been previously damaged: 1) by workers from the same colony (SC), 2) by workers from a different colony of *C. formosanus* (DC), 3) by workers of *Reticulitermes virginicus* (Banks) (R), or 4) no damage (control, C). This laboratory experiment consisted of two parts: a preconditioning period

when wood blocks were damaged by termites of specific colonies and a choice test in which termites were presented with the damaged wood.

Block Preconditioning. *Reticulitermes virginicus* were collected in a fallen pine (*Pinus* sp.) log from the Louisiana State University Idlewild Research Station near Clinton, LA. *Coptotermes formosanus* were collected from five colonies in baldcypress trees (*Taxodium distichum* [L.] Rich.) growing along the Calcasieu River near Lake Charles, LA. Wood blocks were from pine (*Pinus* sp.) lumber, free of knots, and cut to 1.8 by 1.8 by 1.8 cm.

To precondition wood blocks for the choice test, blocks were first oven dried and weighed. Then one hundred sixty glass, screw-top containers (4.7 cm tall by 4.5 cm ID) were established, each with 1.0 g oven dried vermiculite (heat-expanded mica substrate), 2.2 g deionized water, one wood block, and 50 workers (undifferentiated larvae $\geq$ the third instar). There were 16 containers for each of the five colonies of *C. formosanus* and 40 for *R. virginicus*. Additionally, 40 containers were set up identically as above, but without termites, to provide the undamaged control blocks. All containers were maintained in the same bioclimatic chamber at 27.5 ± 1.0° C, 97 ± 1.0% relative humidity, and near-constant darkness until day 10 when the units were dismantled. Wood blocks were brushed clean, oven dried for about 16 h at 88° C, and re-weighed to determine block mass after

preconditioning. Mass change of controls was used to correct other mass values for spurious changes. For each termite-damaged block, the number of surface openings of internally penetrating tunnels was counted. Block damage at this point was only mild to moderate, and all blocks were obviously still valuable as food.

Choice test. Preference of *C. formosanus* for wood previously damaged by termites was tested in a completely randomized design blocked on colony source of termites. *Coptotermes formosanus* from the same five colonies as before were used. Because of a termite shortage, I had to re-use termites from the preconditioning period for one colony; analysis of variance (see below) showed no aberrant trends from these units.

Thirty five test units (4 colonies with 8 units each, 1 colony with 3 units) were established on day 0. Each unit consisted of a plastic friction-top container (3.1 cm tall by 9.3 cm ID) with 6.3 g oven dried vermiculite, 250 workers, 14.2 g deionized water, and four wood blocks, one of each treatment, placed randomly around the edge of the container. For the SC treatment, the units from each colony each received a wood block previously damaged by nestmates. For the DC treatment, each colony was randomly paired with a different colony, then each of its units received a wood block damaged by that particular colony. All units received one of the R blocks and one of the C blocks. Five additional containers

were set up identically as above, but without termites, to provide mass correction factors for the wood blocks as before. All units were maintained in the same bioclimatic chamber as before. On day 21, the units were dismantled, and the blocks were brushed clean, oven dried, re-weighed, and mass-corrected to determine feeding rate (mg wood eaten per day) relative to block mass after the preconditioning period.

Heterogeneity of treatment variances, as determined by Hartley's F_{max} statistic (Winer, 1971) existed for feeding rate and was corrected with weighted analysis of variance (Proc GLM, SAS Institute, 1985, p. 207). Colony effects were blocked, and linear contrast mean separation was used to compare feeding rate among treatments. Treatment by colony interaction was the error term, and differences were accepted at the $\alpha \leq 0.05$ level. Regression analyses (Proc REG, SAS Institute, 1985, pp. 269-336) demonstrated that feeding rate varied significantly with the number of tunnel openings in blocks after the preconditioning period in a model with linear, quadratic, and cubic coefficients. Therefore, these terms were tested as covariates with treatment in an unweighted analysis to discriminate thigmotaxic effects inherent in the treatment effects.

Termite trail-following activity for wood extracts. There is growing evidence that termite trail pheromones often include highly persistent orientation components (Traniello, 1982; Runcie, 1987). It is possible that termites in the

choice test were responding, at least in part, to such cues deposited on wood by termites during the preconditioning period. However, since I oven dried my blocks after the preconditioning period (necessary to accurately measure feeding rate for the choice test), it was uncertain whether any persistent components remained active into the choice test. Therefore, a series of wood block extracts were made and assayed for termite trail-following activity to determine whether pheromonal cues were deposited on wood by *C. formosanus* and whether such cues retained their activity following oven drying.

Blocks of wood were damaged by *C. formosanus* and *R. virginicus* (two blocks for each species) in a method similar to that described in the block preconditioning section. During disassembly of the units, one block from each species was cleaned of debris and termites, split into smaller pieces, then put in 10 ml hexane and passively extracted for 7 days at 0° C (non-oven dried treatment). The remaining block for each species was first oven dried at 94° C for 18-24 hours then similarly extracted (oven dried treatment). An undamaged control block never exposed to termites was oven dried for 24 hours at 94° C then extracted in 15 ml hexane for 8 days (wood control treatment). All wood block extracts were dehydrated with anhydrous magnesium sulfate then concentrated under nitrogen to 1 ml. Additionally, an extract of whole *C. formosanus* workers that was known to have trail-following

activity was used to confirm that the assay could detect trail-following (assay control treatment).

A method similar to the "Open-Field" assay described by Howard *et al.* (1976) was used to test the extracts for termite trail-following activity. Termites for this assay came from the same *C. formosanus* colony used above for extract preparation. About 0.8 µl of each extract was streaked from a 2 µl pipette in a 6.5 cm long semi-circular arc on a ground glass plate. The arc was drawn by following a pencilled outline on a piece of paper under the glass. A 2.7 cm long hexane control streak bisected the arc. A single termite was gently placed on the glass then covered with an inverted petri dish lid. The whole assembly was covered under a sheet of red transparent acetate to simulate darkness. Positive trail-following was recorded if the termite contacted the trail (time = 0 s) then turned onto it and followed it to a terminus within 30 s. I assumed that the probability of a termite randomly following a defined arc in an "open field" was zero. Therefore, any termite following the prescribed trail was judged to be demonstrating a true trail-following response. At least six trials were done for each extract, using one uninitiated termite per trial.

For analysis, data for extracts from the two termite species were pooled by wood block oven treatment, creating four extract treatments: termite damaged, non-oven dried wood; termite damaged, oven dried; undamaged, oven dried; and whole-

termite assay control. Pooling species was justified because *C. formosanus* readily follows trails deposited by *Reticulitermes* spp. (Howard *et al.*, 1976), and, therefore, if persistent cues were a factor in the choice test, *C. formosanus* could have responded to such cues from either species. Response data were placed in two-way crosstabulation tables according to extract treatment and response category (number of termites following trail versus number not). Chi-square analyses were used to test the equality of response frequencies among treatments (Proc Freq, SAS Institute, 1985, pp. 154-155).

RESULTS

Choice test. There were significant differences among treatments for wood feeding rate (F = 15.83; df = 3,12; P = 0.0002, Table 1). There were no colony effects (F = 1.83; df = 4,12; P = 0.1873). *Coptotermes formosanus* preferred wood damaged by conspecifics, regardless of colony, over wood damaged by *R. virginicus* or undamaged wood. Additionally, they preferred wood damaged by *R. virginicus* over undamaged wood. The regression of feeding rate on the number of tunnel openings on wood blocks after the preconditioning period was described by a model (r = 0.64) with linear (slope = 5.17 ± 1.11), quadratic (slope = -0.99 ± 0.36), and cubic (slope = 0.06 ± 0.03) terms. My analyses testing these terms as covariates with treatment showed that 92.1% of the treatment

effect on feeding rate (relative to sum of squares III) was explained by the number of tunnel openings after the preconditioning period, which was (mean ± SEM) 4.5 ± 0.4 for the SC treatment, 3.6 ± 0.4 for the DC treatment, 0.2 ± 0.09 for the R treatment, and 0 for the C treatment.

Termite trail-following activity for wood extracts. Workers of *C. formosanus* demonstrated slight trail-following activity for extracts of wood that had been damaged by *C. formosanus* but not subsequently oven dried (2 positive responses/12 trials). They also had slight activity (3/12) for extracts of wood damaged by *R. virginicus* but not subsequently oven dried. They did not respond to extracts of wood that had been damaged by either *C. formosanus* (0/6) or *R. virginicus* (0/6) then subsequently oven dried, or to extracts of undamaged control wood that had been oven dried (0/6). *Coptotermes formosanus* showed the greatest response for whole-termite extract (7/12). Chi-square tests (Table 2) showed no differences in response among the three wood extract treatments ($\chi^2 = 4.3$; df = 2; $P = 0.119$). However, response for whole-termite extract was significantly higher than that for the wood extracts ($\chi^2 = 14.2$; df = 3; $P = 0.003$), demonstrating the ability of this assay to detect trail-following.

DISCUSSION

In the field, food selection by *C. formosanus* is possibly

influenced by both persistent pheromonal cues (Traniello, 1982; Runcie, 1987) and by thigmotaxic cues. However, in my experiment, *C. formosanus* demonstrated convincing response only to thigmotaxic stimuli. The trail-following response of *C. formosanus* to extracts of termite-damaged wood was always weak and variable or absent if the wood had been oven dried. There is ample evidence for the solubility of trail-active compounds in hexane or similar non-polar solvents (Smythe *et al.*, 1967; Matsumura *et al.*, 1969; Leuthold & Lüscher, 1974; Oloo & McDowell, 1982). Therefore, if trail-active compounds had been present in the oven dried, termite-damaged wood of the choice test, my extracting and concentrating process should have yielded them. It seems that any persistent compounds deposited on wood during the preconditioning period were eliminated by my oven drying process and were absent from the choice test. Therefore, I believe that thigmotaxic stimuli were the primary cues remaining from the preconditioning period and that this study affords an examination of the role of natural thigmotaxic cues on food selection by *C. formosanus* without the confounding effect of persistent pheromones. Although *C. formosanus* will follow trails deposited by *Reticulitermes*, it has failed to convincingly demonstrate trail deposition itself (Howard *et al.*, 1976). Clearly, the role of pheromones in foraging by *C. formosanus* is poorly understood.

Conversely, my covariate analyses clearly demonstrated

that *C. formosanus* responded to thigmotaxic stimuli, as measured by the number of tunnel openings on wood after the preconditioning period. *Coptotermes formosanus* typically bores penetrating tunnels between growth rings of a block, while *R. virginicus* carves depressions on the block surface (Delaplane & La Fage, in press [Chapter 5]). In my present study, blocks damaged by *C. formosanus* had conspicuously more tunnel openings, and when *C. formosanus* were added to the units at the beginning of the choice test they were immediately attracted to and entered blocks with tunnels. Similar thigmotaxic attraction was also documented by Usher (1974) for *Pseudacanthotermes militaris* (Hagen). Although thigmotaxic conditioning of wood blocks by either species made blocks more attractive to *C. formosanus* (relative to unconditioned controls), this species apparently could discriminate damage caused by conspecifics and preferred it over that caused by *R. virginicus*.

One could argue that *C. formosanus* in the choice test were responding to differences in volume inherent in blocks of different types of damage, thus introducing another possible cue at work in my experiment. However, I have unpublished laboratory data for this same population of *C. formosanus* that show no preference by these termites for wood blocks ranging in volume from 7.3 cm^3 to 24.2 cm^3 with constant surface area and termite group size of 500. Furthermore, *C. formosanus* in the field increases foraging response as

resource amount increases (Waller & La Fage, 1987). If this latter principle were at work in my laboratory choice test, one would expect the most feeding at undamaged controls with higher volumes, which did not occur. Therefore, differences in volume are an unlikely factor in my results.

For toxic bait termite control, it is important that baits are highly attractive and not repellent. My data demonstrate a preference by *C. formosanus* for wood damaged by conspecifics. Since thigmotaxic cues were strongly indicated, I suggest that bait blocks for use against this termite should be conditioned to enhance their thigmotaxic cues, perhaps by drilling them to make artificial tunnels. Furthermore, it seems that *C. formosanus* reinfesting a treated building may be more attracted to wood previously damaged by *C. formosanus* than to wood damaged by *R. virginicus*.

TABLE 1. Feeding by *C. formosanus* at wood blocks that had been previously damaged: by termites from the same colony (SC), by a different colony (DC), by *R. virginicus* (R), or no damage (control, C).

Treatment	Feeding Rate (mg/d)[1]	N
SC	13.6 ± 1.3 a	33
DC	11.5 ± 1.0 a	33
R	5.1 ± 0.8 b	32
C	2.4 ± 0.3 c	33

[1]column means (± SEM) with the same letter are not significantly different ($P \leq 0.05$; linear contrast mean separation [SAS Institute, 1985, pp. 193-194]).

TABLE 2. Trail-following response frequencies of *C. formosanus* workers to extracts of termite-damaged wood or of whole termites. Response among the three wood extracts were not significantly different, but response for the whole-body termite extract was different from that of the three other extracts.

Extract	Number responding	Number Not responding
Termite damaged, non-oven dried wood	5	19
Termite damaged, oven dried wood	0	12
Undamaged, oven dried wood (wood control)	0	6
Whole-body termite (assay control)	7	5

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Chapter 5

Wood Excavations of Three Species of Subterranean Termites

Entomol. Exp. Appl. (in press)

SUMMARY

I compared the feeding excavations on wood blocks of three species of subterranean termites, *Coptotermes formosanus* Shiraki, *Reticulitermes flavipes* (Kollar), and *R. virginicus* (Banks). Feeding rate followed the order *C. formosanus* > *R. flavipes* > *R. virginicus*. Wood surface area (mm^2) exposed per unit feeding was higher for *C. formosanus* and *R. flavipes* than for *R. virginicus*. This was caused by the tendency of *C. formosanus* and *R. flavipes* to make internally penetrating tunnels, thereby increasing surface area, whereas *R. virginicus* made bowl- and trough-like depressions on the outside of blocks, sometimes decreasing the size of blocks outwardly without a corresponding high increase in surface area typical with the tunnels of the other species. Consequently, wood surface area was sometimes reduced rather than increased as a result of feeding by *R. virginicus*. Different patterns of wood excavation suggest that these termites have divergent roles in wood decay processes.

INTRODUCTION

Wood excavation by termites and other wood-boring insects plays an important role in wood decay. With dead wood in nature, entry of wood-boring insects often depends on pioneer fungi that break down allelopathic substances in wood, soften it, and improve its nutritional quality (Swift & Boddy, 1984). Once wood-boring insects gain entry, their channelizing activities become the dominant factor regulating decay (Ausmus, 1977). However, many types of insects, including termites, infest cured, construction-grade wood with no evidence of prior fungal modification. In such wood, channelization is probably even more important to degradation. For these reasons, it is desirable to examine the excavations of termites and quantify the surface exposed by these insects as they feed, as this may illuminate different saprotrophic roles among these insects. Surface area of termite-channeled wood is difficult to measure because the cavities are irregular. However, I here report a predictive regression model with which I measured changes in wood surface area resulting from feeding by three rhinotermitids, *Coptotermes formosanus* Shiraki, *Reticulitermes flavipes* (Kollar), and *R. virginicus* (Banks).

MATERIALS AND METHODS

Prediction Model. A standard curve for estimating surface area of termite-excavated wood was made by regressing

the mass of polyurethane wood finish taken up by wood blocks with the known surface area of those blocks. One hundred and nine wood blocks (each 19 by 19 by 19 mm) were cut from a board of cured, construction-grade southern pine (*Pinus* sp.) wood then lightly sanded. Using a drill press, all but 15 blocks were drilled with varying numbers of bores (1 to 16) of varying diameters (1.2 to 2.2 mm). This process yielded blocks of 15 classes of surface area, ranging from 2166 mm^2 (undrilled) to 3717 mm^2 (16 bores, each of diameter 1.7 mm). Blocks were then oven dried, individually immersed for about 20 s in polyurethane (Minwax Co., Inc., Montvale, NJ, USA), drained, oven dried, and lightly sanded; the immersion process was then repeated. These two coats of finish sealed off internal microcavities so that a third and final coat of dilute finish would be restricted solely to the surface of the block. Following a standardized procedure, the blocks were weighed, individually immersed in a 3 : 1 (polyurethane : turpentine) solution, drained, oven dried, and re-weighed to determine the mass of dilute polyurethane on the surface of the block. The third coat was diluted to minimize buildup of finish and to maximize coverage of all internal crevices. The relationship of mass of polyurethane to block surface area was tested with regression analyses (Proc Reg, SAS Institute, 1985b, pp. 269-336) with linear, quadratic, cubic, and quartic coefficients. Only the linear coefficient was significant, and the final prediction equation was $Y = 0.01443X - 3.51825$

($P = 0.0001$; $r = 0.68$), where Y = mass (mg) of polyurethane and X = surface area (mm^2) of wood block. Normality of all mass values was tested and confirmed with the Shapiro-Wilk statistic (Proc Univariate, SAS Institute, 1985a, pp. 350-351), and equality of mass variances was tested and confirmed with Hartley's F_{max} statistic (Winer, 1971). Since mass values were normal with equal variances for each value of surface area, this model was suitable for inversely predicting (Zar, 1974) surface area of termite-excavated blocks similarly treated in polyurethane.

Termites. Termites from three colonies of *R. virginicus* were collected in fallen pine (*Pinus* sp.) logs on 24 May 1988 from the Louisiana State University Idlewild Research Station near Clinton, LA. Termites from three colonies of *R. flavipes* were collected in fallen pine logs on 8 June 1988 at the Harrison Experimental Forest, USDA Forest Service, Southern Forest Experiment Station, near Gulfport, MS. *Coptotermes formosanus* were collected from three colonies in baldcypress trees (*Taxodium distichum* [L.] Rich.) along the Calcasieu River near Lake Charles, LA on 15 June 1988. These colonies of *C. formosanus* in baldcypress trees are routinely fed pine wood in artificial bait stations maintained by this laboratory. The identity of the two *Reticulitermes* species was confirmed by M. I. Haverty, USDA Forest Service, Pacific Southwest Forest and Range Experiment Station, using cuticular hydrocarbon analysis (Howard *et al.*, 1978) and the diagnostic

key of Clément *et al.* (1985).

Bioassay. Experimental wood blocks were cut to the same size and from sapwood of the same board as the blocks used for the prediction model. Blocks averaged 5.2 ± 1.6 (mean ± SD) growth rings, 430 ± 28.9 mg per cm^3 density, and were free of any apparent fungal preconditioning. Cured, construction-grade southern pine (*Pinus* sp.) wood was a suitable substrate for this experiment because it is a preferred food of these termite species in laboratory tests (Smythe & Carter, 1970), and all three species invade such wood in structures in Mississippi and Louisiana.

Patterns of wood excavations of the three termite species were compared in a randomized design. Blocks were oven dried for 28 h at 105° C, weighed, individually soaked in deionized water for about 14 h, then re-weighed. In this manner, the percentage moisture of test blocks was determined to be 81.9 ± 5.0% (dry mass basis) immediately before the start of the bioassay; very moist blocks promote high termite activity and feeding (Delaplane & La Fage, 1989 [Chapter 3]). One hundred forty one test units (3 species by 3 colonies per species by at least 15 units per colony), consisting of glass screw-top containers (4.7 cm tall by 4.5 cm ID), were established on 16 June 1988. There were 47 units per species. Into each unit designated for *C. formosanus* were placed 7.5 g oven dried vermiculite (heat-expanded mica substrate), 17 g deionized water, one wood block, and 300 workers (undifferentiated

larvae ≥ the third instar, of which a sample had been weighed). Into each *Reticulitermes* unit were placed 3.4 g dried vermiculite, 7.7 g deionized water, one wood block, and 300 workers. These conditions provided the optimum population density and moisture conditions for each genus as derived from the data of Lenz *et al.* (1987) while keeping group size constant. One unit for each colony (n = 9) was randomly chosen as a control and did not receive termites. All 141 units were kept in one bioclimatic chamber at 27.5 ± 1° C, 97 ± 1% RH, and near-constant darkness until 27 and 28 June 1988 when the units were dismantled. During disassembly of the units, the number of workers and number of soldiers were counted, and a sample of workers was weighed. Wood blocks were cleaned of debris and termites, oven dried (46 h at 95° C), and weighed.

Surface area (mm^2) of termite-excavated wood blocks was determined by treating the blocks with polyurethane using the standardized procedure then by using the prediction model.

Total percentage group survival and feeding rate (mg wood eaten per g worker per day) were determined. Change in mm^2 block surface area due to termite feeding (ΔS) was calculated by subtracting the mean surface area predicted for the un-excavated control blocks from the predicted surface area of the excavated block. I then calculated ΔS per unit feeding rate. I tabulated for each excavated block the: 1) number of tunnel openings on the surface of the block, 2) number of non

tunnel-like excavations on the surface of the block, and 3) widest diameter (mm) of the largest opening in the end grain.

Statistical Analyses. Analysis of variance with species as treatment and colony effects nested within species as error term was used to test all variables (Proc GLM, SAS Institute, 1985b, pp. 183-260). Differences were accepted at $\alpha \leq 0.05$ level. Heterogeneity of treatment variances, as determined by Hartley's F_{max} statistic (Winer, 1971), existed for all variables except ΔS and number of tunnel openings and was corrected by weighting the analysis with the reciprocal of the treatment variances (Proc GLM, SAS Institute, 1985b, p. 207). Linear contrast mean separation was used to identify treatment differences. For ΔS and number of tunnel openings, the analyses did not require weighting, so least significant difference (LSD) mean separation was used (Proc GLM, SAS Institute, 1985b, pp. 199).

RESULTS AND DISCUSSION

There were differences among species for feeding rate ($P = 0.0017$), ΔS ($P = 0.0105$), ΔS per unit feeding ($P = 0.0493$), number of tunnel openings ($P = 0.0009$), and number of surface excavations ($P = 0.0170$). The three species did not differ in group survival ($P = 0.0683$) or widest diameter of the largest end-grain opening ($P = 0.1554$; Table 1). There were colony effects with all variables ($P \leq 0.0012$; Table 2).

My results support those of Smythe & Carter (1970) who

showed a trend for feeding and survival with these species in the order *C. formosanus* > *R. flavipes* > *R. virginicus*; since the termites in my assay displayed reproducible trends, the experimental conditions were suitable for examining excavation behavior.

My data give new quantitative information on wood excavation by subterranean termites. There were clearly visible differences in the types of excavations made by the three species (Fig. 1). *Coptotermes formosanus* produced more penetrating tunnels and fewer exterior excavations than did either *Reticulitermes* species (Table 1). *Reticulitermes flavipes* made fewer penetrating tunnels than did *C. formosanus*, but its tunnels were often very expansive, constituting hollowed-out chambers within the block; however, the best quantification of this effect (greatest width of largest opening) was not significant, at least partly due to a strong colony effect from one colony of *R. flavipes* with much narrower openings than the other two (Table 2). Of the three species, *R. virginicus* produced the most surface excavations; its tunnels were almost never as penetrating as those of the other species.

Change in block surface area due to termites (ΔS) increased as feeding rate increased (Table 1). However, ΔS was not a direct function of feeding rate but varied somewhat independently. Per unit feeding, *C. formosanus* and *R. flavipes* exposed more mm^2 surface area than did *R. virginicus*

(Table 1). This is explained by the emphasis of *R. virginicus* on surface excavations. The bowl- and trough-like depressions carved by *R. virginicus* as they fed (Fig. 1) sometimes reduced the size of blocks outwardly without a corresponding high increase in surface area typical with the tunnels carved by the other species. Consequently, the surface area of a block was sometimes reduced rather than increased as a result of feeding by *R. virginicus*; the number of data values predicted by my model showing reduction in surface area ($-\Delta S$) were 13 for *R. virginicus* but only 3 for *R. flavipes* and 0 for *C. formosanus*. These predicted values are consistent with the visible patterns of excavations on the blocks and confirm that my model was an effective estimator of surface area. In general, the amount of surface area exposed by termites per unit feeding was governed by the type of excavations made. Internally penetrating tunnels in high number (as with *C. formosanus*) or of expansive size (as often with *R. flavipes*) caused greater surface area exposure than did exterior excavations.

Channelization of wood by insects, with its inherent alteration of wood surface area, is an important regulator of wood decay. Ausmus (1977) documented some of the effects of channelization in logs of a mesic hardwood forest. Following preconditioning fungi, wood-boring insects channelize and break up wood into smaller particles which are favorable substrate for nitrogen-fixing bacteria; it is during

channelization that nitrogen accumulation peaks. This, in turn, sets the stage for intrusion of other invertebrates and for fungal rhizomorphs which export nutrients to other fungal tissues. Thus, channelization regulates both nutrient accumulation and export. However, many insects, including anobiid, bostrichid, and lyctid beetles, carpenter bees, and termites, regularly enter cured, construction-grade wood with no evidence of prior fungal decay. In such wood, it is likely that channelization is even more crucial to succession of other decay organisms.

The termite species in my study may have different saprotrophic roles in the decomposition of wood. In cured wood, *C. formosanus* and *R. flavipes* expose more surface area per unit feeding than does *R. virginicus*. If this reflects general phenomena, it is likely that *C. formosanus* and *R. flavipes* are more effective than *R. virginicus* at exposing wood substrate to other decay organisms. There could also be successional differences with these termites. *Reticulitermes virginicus* could conceivably "open up" the surface of wood, facilitating later tunneling by other species; however, I know of no field data indicating this. *Coptotermes formosanus* and *R. flavipes* are known to occasionally displace each other in single pieces of wood (Thompson, 1985; Su & Scheffrahn, 1988).

Further research is needed to clarify possible interactions of prior fungal modification of wood and subsequent surface exposure by termites. Certain wood-decay

fungi stimulate feeding in *Coptotermes* spp. (French, 1978; Lenz *et al.*, 1980) and in *R. flavipes* (Smythe *et al.*, 1971), and microbial modification seems necessary to de-toxify baldcypress wood for *C. formosanus* in Louisiana (Waller & La Fage, 1987). My results reflect possible decay phenomena in cured wood, a very real ecological arena for these pestiferous species; however, the patterns of surface exposure I observed may be altered in natural wood preconditioned by fungi.

TABLE 1. Bioassay of feeding excavations made by three species of subterranean termites.

Variable	Species[1]		
	C. formosanus	*R. flavipes*	*R. virginicus*
Survival (%)	93.2 ± 0.5a	90.8 ± 0.6a	77.9 ± 1.8a
Feeding rate (mg/g/d)	85.6 ± 1.7a	51.8 ± 0.8b	43.9 ± 1.4c
Change in block surface (ΔS, mm^2)	2205 ± 141a	1138 ± 134b	386 ± 99b
ΔS per unit feeding (mm^2)	25.9 ± 1.6a	22.1 ± 2.6a	8.6 ± 2.4b
No. tunnel openings	34.2 ± 0.9a	8.5 ± 0.9b	7.2 ± 0.7b
No. surface excavations	2.5 ± 0.2c	5.6 ± 0.7b	8.3 ± 0.4a
Width largest opening (mm)	6.6 ± 0.4a	10.9 ± 0.8a	6.8 ± 0.7a

(TABLE 1, cont.)

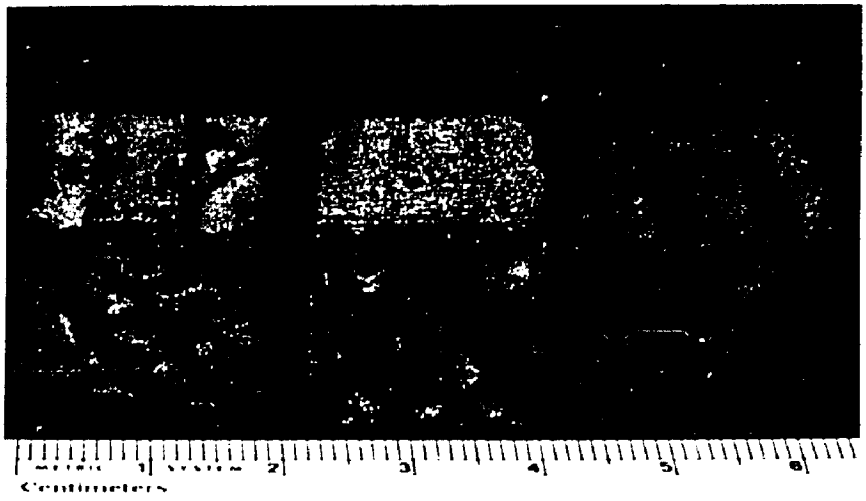
[1]Row means (± SEM) with the same letter are not significantly different ($P \leq 0.05$; linear contrast or LSD [see text] mean separation [SAS Institute, 1985, pp. 193-194, 199]).

TABLE 2. Colony means for measured variables, percentage survival (S), feeding rate (FR, mg/g termite/d), change in block surface (ΔS, mm^2), ΔS per unit feeding (ΔS/FR, mm^2), number of tunnel openings (T), number of surface excavations (EX), and width of largest opening (W, mm).

Species	Col.	S	FR	ΔS	ΔS/FR	T	EX	W
C. f.	1	94.1	72.5	1749	24.1	28.8	3.3	6.7
	2	91.4	93.5	2188	23.6	36.6	1.9	6.7
	3	94.3	89.8	2648	29.7	36.7	2.5	6.3
R. f.	1	90.4	53.3	1934	36.2	11.2	0.5	15.2
	2	92.8	47.0	1031	21.8	12.8	5.1	11.5
	3	89.5	54.5	583	10.8	2.5	10.1	6.0
R. v.	1	87.6	46.4	485	10.8	11.1	6.6	7.4
	2	64.5	46.9	237	4.3	2.6	10.3	9.2
	3	83.1	37.6	446	11.3	8.2	7.8	5.3

FIGURE 1

Wood blocks excavated by (left to right) *C. formosanus*, *R. flavipes*, and *R. virginicus*. *Coptotermes formosanus* made more penetrating tunnels and fewer surface excavations than did either *Reticulitermes* species. Per unit feeding, *C. formosanus* and *R. flavipes* exposed more surface area (mm^2) than did *R. virginicus*.



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Chapter 6

Suppression of Termite Feeding and Symbiotic Protozoans by the Dye, Sudan Red 7B

Entomol. Exp. Appl. 50(3): 265-270

SUMMARY

Laboratory groups of the Formosan subterranean termite, *Coptotermes formosanus* Shiraki (Isoptera: Rhinotermitidae), were fed for 14 days on wood shavings soaked in acetone solutions of 0%, 0.5%, or 1% concentrations of the dye, Sudan Red 7B or on shavings not soaked in acetone (0% non-acetone [NA]). Termites feeding on dyed wood became visibly stained red. Groups of dyed or non-dyed termites were then placed in containers and allowed to feed on non-dyed wood for 21 days. Dyed termites had lower numbers of symbiotic protozoans, lower feeding rates, and lower survivorship than did non-dyed termites. Survivorship was significantly lower in the 1% concentration than in the 0.5% concentration. Covariate analyses suggested that Sudan Red acts both directly and indirectly (via suppression of gut fauna) to reduce vigor in termites. Because there is variable survival response to this dye by different populations of *C. formosanus*, I recommend preliminary tests of dye toxicity before using it extensively in experiments.

INTRODUCTION

The oil-soluble dye, Sudan Red 7B (BASF, Wyandotte Corp.), is a valuable tool for marking subterranean termites in field studies (Su & Scheffrahn, 1988; Su *et al.*, 1984). When workers of *Coptotermes formosanus* Shiraki eat materials stained with this dye, they become visibly stained red. The dye is deposited in fat body, mid- and hindgut, and muscle (Lai *et al.*, 1983) and can remain visible for up to 42 days (Su *et al.*, 1988). As with any animal marker, it is important to confirm that Sudan Red is relatively innocuous to *C. formosanus,* and several researchers have made important steps in this direction. Lai *et al.* (1983) tested the delayed toxicity of Sudan Red after a 13 day exposure to dye and reported no difference in survivorship between dyed groups and controls. Su *et al.* (1983a) found only 3.5% mortality after continuous exposure to dye for 12 days.

However, to my knowledge, there is no information on the feeding rates of termites dyed with Sudan Red. Such data would be useful, considering that feeding rate is one of the most commonly measured variables in termite bioassays. Historically, Sudan Red has been used only in field studies, but its use could certainly extend to laboratory bioassays where feeding rate is more easily and frequently measured. Therefore, in this study, I compared the feeding rates of dyed *C. formosanus* with non-dyed groups and re-examined the dye's effect on survivorship and symbiotic protozoans.

MATERIALS AND METHODS

Wood shavings of pine (*Pinus* sp.) were dyed by soaking them in acetone solutions of 0%, 0.5%, or 1% (weight/weight) concentrations of Sudan Red 7B for four hours then allowing them to thoroughly dry. A fourth set of shavings was not soaked in acetone, constituting a non-acetone control (0% non-acetone [NA]). *Coptotermes formosanus* foragers were collected from five colonies in cypress trees (*Taxodium distichum* [L.] Rich.) growing in water along the Calcasieu River near Lake Charles, Louisiana. Because of the water barrier these colonies are completely contained, and foraging and general movement by termites is limited to the tree itself. About 2800 workers (undifferentiated larvae ≥ the third instar) from each colony were distributed into four glass, screw-top containers (9.2 cm tall by 8.3 cm ID, 700 termites per container), each with 182 g acetone-washed sand, 21 ml deionized water, and ca. 2 g of wood shavings of one of the four treatments. These 20 containers were kept in a bioclimatic chamber at 27.5 ± 1° C and 97 ± 1% relative humidity for 14 days, after which four groups of 125 workers from each treatment/colony combination (80 experimental units) were collected and mean weight per termite determined for each group. Each group was placed in a glass, screw-top container (4.7 cm tall by 4.5 cm ID) with 30 g acetone-washed sand, 3.4 ml deionized water, and a pre-weighed, non-dyed 3.4 cm^3 block of wood (*Pinus* sp.). All 80 units were maintained in the same

bioclimatic chamber as before.

After 21 days, termites were counted and samples of termites weighed. The blocks of wood were brushed clean, oven dried for 65 h at 77° C, and weighed. Wood feeding rate (mg wood eaten/g termite/day) and percentage termite survival were determined. The average number of intestinal protozoans per termite was found with a method modified from Mannesmann (1972). Analysis of variance, blocked on colony, was used to test the variables of interest (SAS Institute, 1985, pp. 183-260). Treatment X colony interaction was the error term, and $\alpha \leq 0.05$ was accepted as different. Heterogeneity of treatment variances was detected for survivorship and number of protozoans with Hartley's F_{max} statistic (Winer, 1971) and was corrected by weighting the analysis with the reciprocal of the treatment variances (SAS Institute, 1985, p. 207). Linear contrast mean separation was used to identify treatment differences. For feeding rate, the analysis did not require weighting, so LSD mean separation was used (SAS Institute, 1985, p. 199).

RESULTS AND DISCUSSION

There were significant differences among treatments in all variables of interest (Table 1). Termites dyed with Sudan Red 7B had lower numbers of protozoans, lower feeding rates on non-dyed wood, and lower survivorship than did either non-dyed group (Table 2). Number of protozoans and feeding rate

were not different between the 0.5% and 1% concentrations, but survivorship was lower in the 1% concentration. Feeding rate and survivorship were not different between the 0% non-acetone and 0% treatments, but number of protozoans was lower in the 0% group. Colony effects were never significant, but treatment X colony interactions occurred with feeding rate and survivorship (Tables 1 and 3). With feeding rate, this interaction was largely from colony 5 which showed a smaller change between the 0% and 0.5% treatments than did the other colonies; with survivorship, colony 3 showed a relatively uniform response across treatments (Table 3).

Lai *et al.* (1983) also found reduced protozoan numbers in dyed *C. formosanus*; however, they concluded that termite density in the staining chambers was more important than dye in affecting protozoan numbers. But, when I subjected their data to main-effects analysis blocked on time (Proc ANOVA, SAS Institute, 1985, pp. 57-82), I found that dye ($P = 0.0087$) and length of exposure to dye ($P = 0.0422$), rather than termite density ($P = 0.0835$), affected protozoan numbers. In Lai *et al.*'s study, dyed termites had significantly fewer protozoans than did non-dyed termites, and the number of protozoans decreased as exposure was prolonged. Therefore, my data and those of Lai *et al.* agree that Sudan Red reduces the number of protozoans in *C. formosanus*. In my study, feeding rate was accompanied by a similar drop in protozoan numbers, raising the possibility that feeding was affected by

both the dye and the simultaneous loss of gut fauna. To discriminate these factors, I compared the analysis of variance sum of squares for dye treatment with that for dye treatment adjusted for a protozoan covariate. This suggested that 49.6% of the suppressing effect of dye on feeding was explained by its simultaneous depression of protozoans. When the protozoan complements of non-dyed *C. formosanus* are altered or eliminated, termite feeding decreases (Smythe & Mauldin, 1972). Therefore, it seems that Sudan Red suppresses termite feeding at least in part by lowering protozoan numbers. However, direct suppression of termite appetite by Sudan Red is still likely, and, indeed, the dissected guts of dyed termites were usually less distended than those of non-dyed groups.

My data for survivorship (Table 2) generally support those found by Su *et al.* (1983a) for *C. formosanus* in Louisiana under similar conditions. In their study, termites exposed to 2% dye for up to 12 days and subsequently maintained on non-dyed wood for one month had only 43.6% survivorship. However, Hawaiian *C. formosanus* exposed to 0.5% or 1% dye for 13 days and then kept on non-dyed food (for an indeterminate length of time) survived as well as did control groups (Lai *et al.*, 1983), and *C. formosanus* from Florida exposed to 1% dye for 10 days and kept on non-dyed wood for 4 weeks had 88% survivorship (Su *et al.*, 1988). This variation in the survival response of *C. formosanus* may arise

from genetic differences in populations or physiological differences due to habitat (subterranean nests in Hawaii and Florida versus partially submerged trees in Louisiana). Since abnormally faunated *C. formosanus* have higher mortality (Smythe & Mauldin, 1972), I again analyzed the effect of protozoans as a covariate with dye treatment. This time, 64.1% of the effect of dye treatment on survival was explained by changes in the number of protozoans. Therefore, it seems that Sudan Red reduces feeding and survival in *C. formosanus* directly as well as indirectly via suppression of gut fauna.

The two control treatments differed only in the numbers of protozoans, with fewer protozoans in termites fed acetone-treated (extracted) wood (0%). Heartwood of certain American tree species (Carter *et al.*, 1981) and extracts from certain Brazilian hardwoods (Carter *et al.*, 1983) have anti-protozoal properties in *C. formosanus*, but, to my knowledge, there is no information on extracts of *Pinus* spp. that are favorable to protozoans. In my data, the negative effect of Sudan Red on protozoans may have been augmented by the extraction of a protozoan-favoring component from the *Pinus* shavings.

My present data agree with preliminary work that showed suppression of protozoans, feeding rate, and survivorship of *C. formosanus* by Sudan Red, using 0.5% and 1% levels and only a non-acetone control (Delaplane *et al.*, 1988). Such reproducibility strengthens my conclusion that Sudan Red is not totally innocuous to *C. formosanus*.

Although my data indicate deleterious effects of Sudan Red 7B on *C. formosanus*, this dye remains the best marker available for use by termitologists. With some termite populations it causes relatively low mortality (Lai *et al.* 1983; Su *et al.*, 1988). Furthermore, it remains visible for at least 42 days (Su *et al.*, 1988) and is not exchanged by trophallaxis (Su *et al.*, 1983b). Nevertheless, my data show a clear suppression of feeding in dyed termites. In feeding bioassays using Sudan Red, this source of variation must be controlled. Since the literature, as well as my data, reveals variation in survival response by *C. formosanus* to this dye, I recommend preliminary tests of dye toxicity before using it extensively in experiments.

TABLE 1. Analysis of variance testing the effects of Sudan Red 7B (tmt) and source colony (col) on termite vigor.

Variable	Source	DF	F	P > F
Number of protozoans	tmt	3	8.8	0.0023
	col	4	0.9	0.4740
	tmt X col	12	1.6	0.1302
Feeding rate	tmt	3	18.1	0.0001
	col	4	2.1	0.1459
	tmt X col	12	5.7	0.0001
Survivorship	tmt	3	8.5	0.0027
	col	4	1.2	0.3473
	tmt X col	12	7.1	0.0001

TABLE 2. Effects of the dye, Sudan Red 7B, on workers of *C. formosanus*.[1] Termites were exposed to either dyed or non-dyed wood for 14 days then fed on non-dyed wood for 21 days.

Treatment[2]	Number of Protozoans	Feeding rate (mg/g/day)	Percentage Survivorship
0 (NA)	2000.0 ± 236.1 a	29.0 ± 1.3 a	89.4 ± 2.1 a
0	1305.9 ± 257.9 b	29.2 ± 1.8 a	87.6 ± 2.6 a
0.5	704.0 ± 112.2 c	15.0 ± 1.0 b	59.0 ± 5.5 b
1	523.1 ± 146.0 c	15.3 ± 0.9 b	38.7 ± 7.5 c

[1]Overall means (± SEM) across 5 colonies. Those in a column followed by the same letter are not significantly different at the $\alpha \leq 0.05$ level.

[2]Percentage concentration (wt/wt) of dye-acetone solutions used for dye treatments (0, 0.5, and 1%), or a non-acetone control (0 [NA]).

TABLE 3. Colony means (± SEM) for tested variables. Treatment abbreviations are described in Table 2.

Treatment	Colony	Number of Protozoans	Feeding Rate (mg/g/day)	Percentage Survival
0 (NA)	1	1900.0 ± 208.2	36.2 ± 3.5	93.3 ± 1.2
	2	1625.0 ± 692.1	31.9 ± 1.0	97.0 ± 1.4
	3	1966.7 ± 841.3	26.8 ± 1.4	76.0 ± 0.8
	4	2725.0 ± 272.0	22.6 ± 1.1	84.2 ± 3.0
	5	1666.7 ± 405.5	28.8 ± 0.9	95.5 ± 0.7
0	1	750.0 ± 322.8	40.4 ± 2.5	94.8 ± 1.2
	2	1550.0 ± 50.0	30.2 ± 1.9	92.4 ± 1.2
	3	1166.7 ± 333.3	25.8 ± 0.7	75.7 ± 2.1
	4	2225.0 ± 864.5	24.6 ± 0.7	80.8 ± 7.6
	5	925.0 ± 390.3	24.6 ± 2.2	93.6 ± 2.6
0.5	1	800.0 ± 57.7	12.9 ± 0.7	57.3 ± 1.9
	2	50.0 ± 50.0	15.9 ± 1.1	18.7 ± 5.1
	3	433.3 ± 33.3	13.8 ± 2.1	76.0 ± 2.6
	4	800.0 ± 173.2	11.2 ± 1.0	67.2 ± 2.0
	5	1090.0 ± 242.4	19.6 ± 1.6	71.6 ± 5.3
1	1	200.0 ± 57.7	12.7 ± 2.8	44.3 ± 17.0
	2	300.0 (1 obs.)	18.9 ± 1.4	6.7 ± 5.1
	3	700.0 ± 251.7	15.7 ± 1.2	73.3 ± 2.5
	4	133.3 ± 88.2	12.9 ± 2.4	20.2 ± 8.8
	5	1133.3 ± 375.7	16.4 ± 1.0	51.0 ± 17.1

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CONCLUSIONS

These studies have generated new information on feeding and foraging behaviors of subterranean termites, some of which is helpful for designing toxic bait control strategy.

Termites are tenacious foragers. When presented with a choice of equivalent food items, *C. formosanus* concentrates foraging efforts at items discovered early. This suggests a sort of chronological priority given by termites to the first favorable food they encounter. This chronological priority, or tenacity, differs among species, may be a mechanism for niche separation in termite communities, and may be energetically cost-effective when balanced against the costs of exploratory foraging. When *C. formosanus* is presented with wood blocks differing in moisture content, they prefer blocks with the highest initial moisture. Therefore, when presented with non-equivalent food items, termites select more on the basis of food quality than on chronological priority. Termites remain tenacious at initially favorable food even if its quality deteriorates with time to a level equivalent to other nearby choices.

These results have important implications for toxic bait control. Termites are likely to forage tenaciously at a few sites rather than superficially at many sites. Therefore, one might successfully control termites at a structure with only a few well-placed baits. Since termites forage heavily at sites they discover early, it is best to locate and place

baits at the site of initial entry.

When presented with wood blocks of varying moisture content, *C. formosanus* eats higher quantities of highly moist wood. These termites are able to relocate free water. The palatability of toxic bait blocks may be improved by keeping them highly moist, and areas of buildings with damp wood are especially vulnerable to termite attack. *Coptotermes formosanus* can discriminate between wood damaged by *C. formosanus* and that damaged by *R. virginicus* and prefers that damaged by conspecifics. *Coptotermes formosanus* responds favorably to enhanced thigmotaxic cues on wood, and the palatability of toxic baits may be improved by drilling them with holes. Areas of a structure with old termite damage may be especially attractive to reinfesting termites.

Coptotermes formosanus and *R. flavipes* expose more surface area per unit feeding than does *R. virginicus*. This is explained by distinctive types of excavations. *Reticulitermes virginicus* makes exterior excavations that sometimes reduce the size of wood without increasing its surface area, whereas the penetrating tunnels of *C. formosanus* and *R. flavipes* increase surface area. These species may differ in their ecologic roles as wood decomposers.

Workers of *C. formosanus* dyed with Sudan Red 7B have reduced numbers of symbiotic protozoans, feeding rates, and survivorship. Although Sudan Red is the best termite marker available to researchers, it is not totally innocuous.

Because the effects of Sudan Red vary across populations of *C. formosanus*, I recommend preliminary tests of dye toxicity before using it extensively in field tests.

APPENDIX

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Good luck on completing your degree. It was shocking to hear of Jeff's death. If you need another termite expert to fill in on your committee, I will be glad to come down. However, I am going down to Costa Rica about 24 December and I won't be back until a similar time in January.

Sincerely,

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VITA

Keith Scott Delaplane was born to James E. and Barbara J. Delaplane on June 10, 1961, at Logansport, Indiana. For several delightful years he worked on the family grain and livestock farm, raised dairy goats, and built up a 50-hive beekeeping operation. He graduated from Logansport High School in 1979, attended Butler University briefly as a music major, then transferred to Purdue University where he graduated with a BS degree in Animal Science in 1983. In the same year he married the former Mary Florence Burket of Lafayette, Indiana.

In 1984, the Delaplanes moved to Baton Rouge where Keith completed his MS degree in entomology from Louisiana State University in 1986. His thesis research was directed by Dr. John R. Harbo and dealt with phenomena in queenless honey bee colonies. In 1986, Mr. Delaplane began working as a research associate in the urban entomology laboratory of Dr. Jeffery P. La Fage. In this capacity, Keith pursued his PhD part-time. As a research associate, he coordinated numerous non-dissertation projects, including a two-year study of termite feeding at Lake Charles, efficacy tests of insecticides, a study of pestiferous crickets at a paper mill, and a survey of the density of *C. formosanus* in the French Quarter of New Orleans. Also in this position, he gave presentations at scientific meetings in Canada, Spain, and Finland and traveled to the campus of Washington State University for a cooperative

test of an insect detection device.

Mr. Delaplane is a member of the International Research Group on Wood Preservation, Entomological Society of America, Southwestern Entomological Society, Sigma Xi, Gamma Sigma Delta, Ceres, and Alpha Sigma Phi. He is a bagpiper for the Caledonian Society of Baton Rouge and a member of Southside Baptist Church where he serves as a deacon. Keith has accepted a position as Assistant Professor/Extension Entomologist at the University of Georgia.

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Major Field: Entomology

Title of Dissertation: Feeding and foraging behaviors of subterranean termites (Isoptera: Rhinotermitidae)

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